A REVISION OF THE SPECIES OF LAFOEIDAE AND HALECIIDAE (COELENTERATA: HYDROIDA) RECORDED FROM BRITAIN AND NEARBY SEAS



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By P. F. S. CORNELIUS

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SYNOPSIS

Nominal species of hydroids belonging to the families Lafoeidae and Haleciidae recorded from Britain and neighbouring seas are revised. Three species of Lafoeidae and nine species of Haleciidae are accepted.

INTRODUCTION

IDENTIFICATION guides covering the Hydroida faunas of the majority of countries bordering the southern North Sea have appeared during the last fifty years (Broch, 1927, 1928; Kramp, 1935; Vervoort, 1946; Leloup, 1952). In contrast the most

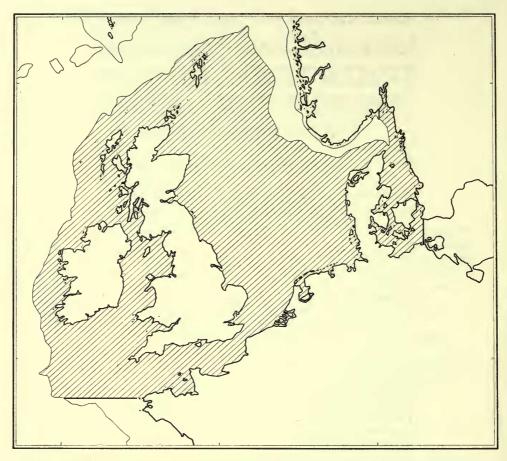


Fig. 1. Map of part of western Europe showing the faunal area (cross-hatching), delimited in most places by the 100 fm (183 m) depth contour (continuous thin line).

recent work describing all the hydroids of British coastal waters is that of Pennington (1885) in which the hydroid chapters were based largely on the monographs of Hincks (1868) and Allman (1871). Perhaps owing to the excellence of its illustrations Hincks' somewhat outdated work still often serves as an identification guide to the British thecate hydroids. The large amount of European work produced during the present century makes a systematic revision of the British hydroids now timely, and two of the thecate/leptomedusan families are revised here.

All nominal taxa of hydroids of the families Lafoeidae and Haleciidae recorded from the area defined below are evaluated. No new species are proposed. Indeed, it seems necessary to interpret the specific limits of some species more widely than hitherto, and some features previously regarded as good specific characters are shown to be unreliable.

A redefinition of the family Lafoeidae was given recently by Naumov (1960, 1969). He did not, however, treat the genus <code>Hebella</code> Allman (1888: 39), which has unclear affinities. It has variously been included in the families Campanulariidae (by Allman, 1888) and Lafoeidae (by Ralph, 1958; Vervoort, 1968, 1972), and removed to a separate family, the Hebellidae (by Nutting, in Fraser, 1912; Nutting, 1927; Fraser, 1937, 1944, 1946). The Hebellidae was established to accommodate genera with separate gonothecae, a hydrothecal diaphragm and a conical hypostome to the hydranth (said to be spherical in Campanulariidae). The two originally included genera, <code>Hebella</code> and <code>Scandia</code> Fraser (1912: 371), were separated as having respectively free medusae and fixed sporosacs. It seems logical at present to retain the family Hebellidae to accommodate these two genera, which are implicitly excluded from the Lafoeidae in Naumov's diagnosis also. The British records of <code>Hebella</code> are discussed below under <code>Lafoea dumosa</code>. None appears valid.

The faunal area outlined in Fig. I corresponds approximately with the continental shelf. Unavoidably it is arbitrary, some species being limital and none restricted to it. It was found that to include the whole of the English Channel, southern North Sea and all Danish waters would add only a few species to the list of all thecate hydroids known from Britain, whereas to include the coast of Norway would add sub-arctic species. Oslofjord and the whole of the Swedish west coast are included. To the south the latitude of the Isle d'Ouessant (Ushant) forms the boundary, so that the whole of the English Channel is included; while to the west, north and north-east the I83 m (600 ft) depth contour provides the arbitrary limit. Taking the thecate hydroid fauna as a whole there appears to be only a few species confined to the deeper parts of the area thus defined, and the British species form, therefore, a recognizable continental shelf assemblage.

The material used was drawn mainly from the collections of the British Museum (Natural History), and carries registered numbers of the format 1894.3.5.11. The numbers reflect the approximate dates, in reverse, on which the specimens were registered and not the dates of collection or deposition in the Museum. Specimens loaned from other museums are so indicated.

Scientific names of British algae mentioned follow the checklist of Parke & Dixon (1968).

Family LAFOEIDAE Hincks, 1868

DIAGNOSIS. Colony stolonal or erect and branching; hydrothecae tubular, even rimmed, without operculum, with or without diaphragm, pedicellate or sessile, adnate in some species; hydranth with conical hypostome; gonothecae aggregated as scapus or coppinia; sexual generation a fixed sporosac.

Type genus. Lafoea Lamouroux, 1821.

Remarks. Naumov (1960, 1969) has proposed two sub-families, diagnosed as follows:

Subfamily EULAFOEINAE. Lafoeidae lacking hydrothecal diaphragm; gonosome in form of coppinia (type-genus *Lafoea* Lamouroux, 1821).

Subfamily LICTORELLINAE. Lafoeidae with hydrothecal diaphragm; gonosome in form of scapus (type-genus *Lictorella* Allman, 1888). In the present area only the first subfamily is represented.¹

Sub-family EULAFOEINAE Naumov, 1960

With the characters discussed immediately above.

Genus FILELLUM Hincks, 1868

Campanularia: Hassall, 1848: 2223.

Capsularia: Gray, 1848:151 (part); Naumov, 1960:280; Naumov, 1969:303; [non Capsularia Cuvier, 1797:665 (= Coryne Gaertner, in Pallas, 1774) (Lamouroux, Saint-Vincent & Deslongchamps, 1824:224); Gray, 1848:88 (= Lafoea Lamouroux, 1821); see Remarks]. Reticularia Thomson, 1853:443; Rees & Thursfield, 1965:85 (part).

Filellum Hincks, 1868: 214 [nom. nov. pro Capsularia: Gray, 1848 (part)]; Vervoort, 1972: 50. Grammaria: Vervoort, 1946: 194 (part).

DIAGNOSIS. Colony comprising a creeping, irregularly-branched stolon bearing hydrothecae without pedicels. Hydrothecae tubular, curved centrally, without operculum. Gonothecae borne in hermaphrodite coppiniae typical of the subfamily.

Type species. Campanularia serpens Hassall, 1848 (Hincks, 1868, by monotypy; Naumov, 1960: 280; Naumov, 1969: 303).

Remarks. The genus Capsularia Cuvier, 1797, was considered by Naumov (1960, 1969) to be identical with Filellum Hincks, 1868. This seems unlikely, however, since Cuvier stated that the hydranths in Capsularia were non-retractile. Capsularia was referred to Coryne Gaertner, in Pallas, 1774, by Lamouroux, Saint-Vincent and Deslongchamps (1824:220), and this synonymy was discussed and accepted by Bedot (1901:437). Gray (1848:61) also included Capsularia in the synonymy of Coryne, but elsewhere in the same work (pp. 85–88, 151) used the name for species now included in other genera and also (p. 151) for the generic name of the species here called Filellum serpens (Hassall, 1848).

Vervoort (1972: 50) showed the name *Reticularia* Thomson, 1853, to be preoccupied by the brachiopod name *Reticularia* McCoy, in Griffith, 1844.

Filellum serpens (Hassall, 1848)

(Fig. 2)

Campanularia serpens Hassall, 1848: 2223; Hassall & Coppin, 1852: 163, pl. 21, fig. 4. Capsularia serpens: Gray, 1848: 151.

Reticularia immersa Thomson, 1853: 443, pl. 16a, figs 2-3.

¹ The species Zygophylax pinnata (Sars, 1874), from the second sub-family, has yet to be recorded from the area and appears seldom to occur within Continental Shelf depths in Europe. Although Kramp (1935) suggested the species might occur in northern Danish waters there are apparently still no records (K. W. Petersen, pers. comm.). It has, however, been recorded from a depth of 90 m in Hardanger Fjord, W Norway (Broch, 1918) and from N Biscay at 186 m depth (Billard, 1923). A statement that the species occurs along 'the entire coast of Europe from [the] Bay of Biscay' northwards (Naumov, 1969) seems erroneous.

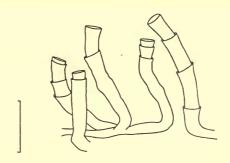


Fig. 2. Filellum serpens. Part of colony, W Scotland (1967.11.10.5). Scale = 500 μm.

Filellum serpens: Hincks, 1868: 214-215, pl. 41, fig. 4 (syn. Reticularia immersa Thomson); Naumov, 1960: 281, figs 47, 170, 171; Naumov, 1969: 303, figs 47, 170, 171; Vervoort,

1972:49-50.

Lafoea abietina: Billard, 1904: 164 (see Remarks).
Grammaria serpens: Vervoort, 1946: 194-196, fig. 82.
Reticularia serpens: Rees & Thursfield, 1965: 87-88.

Type material. Holotype: Dublin, 1842, infertile colony on herbarium specimen of *Abietinaria abietina* (Linnaeus, 1758), coll. A. H. Hassall, 1973.10.8.4; mentioned Gray, 1848: 151.

OTHER MATERIAL EXAMINED. Vattlestraumen, Espegrend, nr Bergen, Norway, 30-40 m, 15 Aug. 1962, colony on Abietinaria abietina, infertile fragments in spirit and coppinia on microslide, coll. W. J. Rees, 1962.11.7.10. Väderö Islands, Sweden, I Oct. 1964, colony teased from substrate, on microslide, coll. W. J. Rees, 1967.11.10.6. Gåsö Ranna, Gullmarfjord, Sweden, 20-30 m, infertile colony on Abietinaria abietina, in spirit and on microslide, coll. W. J. Rees, 1962.11.8.14. Newhaven, nr Leith, Edinburgh, Scotland, infertile colony on Abietinaria abietina, dried material, holotype of Reticularia immersa Thomson, 1853, 1922.6.19.6. Off Millport, Great Cumbrae Island, Bute, Scotland, 40 m, infertile colonies on Kirchenpaueria pinnata (Linnaeus, 1758) and Nemertesia ramosa (Lamarck, 1816), 10 Sep. 1970, coll. C. Edwards, 1971.5.11.33. Off lighthouse, Little Cumbrae Island, 31 Jul. 1966, infertile colony on unidentified substrate, microslide, coll. W. J. Rees, 1967.11.10.5 (Fig. 2). 'Ireland', 13 Jan. 1902, infertile colony on Abietinaria abietina, microslide, coll. E. T. Browne, 1959.9.17.119. False Bay, Republic of South Africa, fertile colony on Amphisbetia operculata (Linnaeus, 1758), spirit, coll. N. A. H. Millard, 1957.4.26.37 (mentioned Millard, 1957: 203).

Description. Colony stolonal, tortuous; branching frequent and irregular with hydrothecae at irregular intervals. Hydrothecae tubular, wider than stolons, bent upwards at $60-90^{\circ}$ approximately in centre; rim even, sometimes flared, without operculum; renovations frequent; basal $\frac{1}{4}-\frac{2}{3}$ of hydrotheca adnate, narrower (Naumov, 1960, 1969), wider (Vervoort, 1972) or same width as upper part. Hydrothecae more or less spaced out depending on amount of substrate available (Hincks, 1868). Hydranth greenish (Hincks, 1868) or lemon-yellow (Hamond, 1957);

tubular, with conical hypostome; 9-12 tentacles, alternately elevated and depressed. Gonothecae borne in hermaphrodite coppiniae typical of the sub-family.

MEASUREMENTS. See Table 1.

	E SCOTLAND (holotype of R. immersa Thomson)	W SCOTLAND (1967.11.10.5)	IRELAND (1959.9.17.119)	Norway (1962.11.7.10)
Hydrotheca				
Diameter at rim	90-140	100-175	115-135	_
Length of free part	_	200-900	80-170	_
Length of attached part	_	200-300	220-300	_
Hydrorhiza				
Diameter of stolon	6o*	100	100	_
COPPINIA (young)				
Overall length	—	_	_	c. 1500
Overall width	_	_	_	c. 1000

^{*} Dried material.

Variations. Hydrothecae in this species are longer in some specimens than in others, long hydrothecae usually being those with one or more renovations. The hydrothecal rim appears to be flared in some specimens and simply tubular in others, with intermediate conditions. The angle at which the distal portion of the hydrotheca is raised varies approximately between 60° and 90°. The proportion of the hydrotheca which is adnate varies between \(\frac{1}{4}\) and \(\frac{2}{3}\) of the total length. Hydrothecae may be either narrower (Naumov, 1960, 1969) or wider (Vervoort, 1972) basally than distally, or of uniform diameter. Hydranth colour has been recorded as greenish (Hincks, 1868) and lemon yellow (Hamond, 1957). Colonies growing in a limited space – as on another hydroid colony – have the hydrothecae closer spaced than in colonies with ample substrate – as on a bivalve shell (Hincks, 1868).

REPRODUCTIVE SEASON. Fertile material recorded April-August off Norfolk (Hamond, 1957), April off NW France (Teissier, 1965), mid August off Norway (1962.11.7.10).

DISTRIBUTION. Common throughout the area.

Habitat. Sublittoral to edge of continental shelf; apparently not recorded intertidally. Recorded growing most frequently on sertularian hydroids, especially Abietinaria abietina, but also Hydrallmania falcata (Linnaeus, 1758) and Sertularia cupressina Linnaeus, 1758. Also occurs on non-living substrates such as bivalve shells. Hincks' (1868) statement that the species is parasitic almost certainly referred to the growth of the species over other hydroids, and was probably not intended to imply an association of living tissues.

REMARKS. Many authors have considered the two nominal species *Filellum serpens* (Hassall, 1848) and *Reticularia immersa* Thomson, 1853, to be conspecific and the present examination of type material of both species supports this view.

The material recorded by Billard (1904:164) from Cherbourg as Lafoea abietina is here identified as Filellum serpens. The specimen was a lafoeid growing over a colony of a sertularian hydroid, Abietinaria abietina. Billard stated that it resembled a colony of F. serpens except that the hydrothecal aperture was not flared (élargie), and hence concluded that the specimen was a stoloniferous growth of Grammaria abietina. Such colony habit has not otherwise been recorded from G. abietina, and it is now known (present paper) that hydrothecae of F. serpens are not invariably flared. G. abietina is, therefore, unrecorded from the English Channel (see p. 384).

Genus GRAMMARIA Stimpson, 1854

Grammaria Stimpson, 1854:9; Broch, 1918:18; Totton, 1930:161; Vervoort, 1946:194 (part); Naumov, 1960:283; Vervoort, 1972:56.

Salacia: Hincks, 1868: 211; [non Salacia Lamouroux, 1816: 212; Stechow, 1922: 150; Rees & Thursfield, 1965: 149; = Thuiaria Fleming, 1828 (see Remarks)].

Reticularia: Rees & Thursfield, 1965: 85 (part).

Type species. Grammaria robusta Stimpson, 1854 (= Campanularia abietina Sars, 1850; by designation by Totton, 1930).

DIAGNOSIS. Hydrocaulus polysiphonic, branched; hydrothecae tubular, outward-curving, even-rimmed, lacking operculum and diaphragm, arranged in longitudinal rows; with hermaphrodite coppiniae.

Remarks. The name Salacia Lamouroux, 1816, was used for the present genus by Hincks (1868). The type species of Salacia is S. tetracythara Lamouroux, 18162 (by monotypy). The type material was examined by Deslongchamps (in Lamouroux, Saint-Vincent & Deslongchamps, 1824) who criticized Lamouroux' description as inaccurate and commented that the vase-shaped gonotheca of the specimen, shown clearly in the original illustration, suggested its affinities were with the genus Sertularia Linnaeus, 1758. Later Bale (1884) examined the same specimen and referred it to Thuiaria Fleming, 1828. Bale also provided a new trivial name, calling the species Thuiaria fenestrata. Like Deslongchamps, Bale considered Lamouroux' description to be inaccurate and, somewhat illogically, regarded Salacia as unavailable. In this he was followed by Bedot (1901), who did not see the specimen. Billard (1909) did see the specimen and confirmed that it had the characters of the genus Thuiaria which name he employed although it was junior to Salacia. Stechow (1922, 1923) seems to have been the first to have included Thuiaria in the synonymy of Salacia, his usage being followed by Rees & Thursfield (1965). Unfortunately the type material of Salacia tetracythara was destroyed along with the bulk of the Lamouroux collection at Caen by a bomb on 7 July 1944 (Redier, 1967), but there would seem little doubt from the available evidence that Salacia is a senior synonym of Thuiaria. Hincks (1868) thus seems to have been unjustified in including the genus Grammaria Stimpson, 1854, in the synonymy of Salacia. The earliest available name for the present genus is thus Grammaria

Totton (1930: 161) nominated *G. robusta* Stimpson, 1854, as genotype. It appears to be conspecific with *G. abietina* (Sars, 1850).

² Various subsequent authors have spelt the specific name tetracyttara.

Vervoort (1946) and Rees & Thursfield (1965) regarded as congeneric the two genera here called *Grammaria* and *Filellum*. The distinction adopted here, however, follows Vervoort's more recent opinion (1972) that colony habit is of generic value. Nevertheless further information on the life-cycles of the species concerned and of other species of Lafoeidae may show this generic distinction to be inappropriate.

Grammaria abietina (Sars, 1850)

(Fig. 3)

Campanularia abietina Sars, 1850: 139.

Grammaria robusta Stimpson, 1854: 9, pl. 3, fig. 1.

Grammaria ramosa Alder, 1856: 361-362, pl. 14, figs 1-4.

Salacia abietina: Hincks, 1868: 212-213, pl. 41, fig. 3 (syn. G. robusta Stimpson).

Grammaria stentor Allman, 1888: 48, pl. 23, figs 1, 1a; Hartlaub, 1905: 599-600, fig. V² (syn. G. intermedia Pfeffer); Jaderholm, 1905: 22-23, pl. 8, figs 4-5 (syn. G. intermedia Pfeffer) (syn. nov.); [? non Grammaria stentor: Linko, 1911: 140-143, fig. 23; Naumov, 1960: 282-283, fig. 173; Naumov, 1969: 305-306, fig. 173; (see Remarks)]; (syn. nov.).

Grammaria magellanica Allman, 1888: 48-49, pl. 23, figs 2, 2a-b; Vervoort, 1972: 58-60, fig. 166; (syn. nov.).

Grammaria insignis Allman, 1888: 49, pl. 23, figs 3, 2a-b; (syn. nov.).

Grammaria intermedia Pfeffer, 1889: 53-54.

Grammaria abietina: Broch, 1917: 1-16, figs A-C, pls 1-2; Broch, 1918: 18-21; Kramp, 1935: 127-128, fig. 55; Naumov, 1960: 283-284, fig. 174; Naumov, 1969: 306-307, fig. 174; Calder, 1970: 1523, pl. 5, fig. 1; Vervoort, 1972: 56 (syn. G. robusta Stimpson). Grammaria abietina var. brevicyatha Broch, 1918: 20-21, fig. 5.

Reticularia abietina: Rees & Thursfield, 1965: 85-86 (syn. G. robusta Stimpson).

Type material and locality. Colony 25 mm high, near Bergen, Norway, 55-75 m, summer of 1849 (Sars, 1850); specimen not located.

MATERIAL EXAMINED.³ North Atlantic: Carl Island and Cape Torell, Spitzbergen, colony in spirit, coll. A. E. Eaton, 1874.4.4.59a. Unnamed locality, Spitzbergen, fragments of colonies in spirit, coll. A. E. Eaton, 1874.4.4.64. E of Faroes, 62°01′ N, 5°19′ W, 210 m, 1869, two colonies in spirit, coll. H.M.S. 'Porcupine', via A. M. Norman coll., 1912.12.21.303. Trondheim Fjord, Norway, 1893, fragments of hydrocauli in spirit and I microslide (Fig. 3), via A. M. Norman coll., 1912.12.21.599. Brattholmen, Hjeltefjord, Espegrend, nr Bergen, Norway, 40-90 m, 9 Apr. 1962, infertile part of colony in spirit and one coppinia on microslide, coll. W. J. Rees, 1962.10.7.23. Off Huglin, Hardanger Fjord, Norway, 180 m, 1879, several colonies in spirit, via A. M. Norman coll., 1912.12.21.305. Shetland Isles, 1861, several colonies in spirit, coll. A. M. Norman, 1912.12.21.302. Northumberland coast, branched colony on herbarium sheet, coll. J. Alder, Hancock Museum, Newcastle-upon-Tyne [syntype of Grammaria ramosa Alder, 1856; figured, Alder, 1856: pl. 14, fig. 1 (J. B. Garfath, pers. comm.)]. Dried colony in glass tube, Northumberland coast, coll. J. Alder, 1857.8.3.52 [syntype of Grammaria ramosa Alder, 1856]. Northumberland, branched hydrocaulus in spirit, coll. J. Alder, via A. M. Norman coll., 1912.12.21.301 (? mentioned, Hincks, 1868:213).

³ With the exception of 1962.10.7.23 all material listed is infertile.

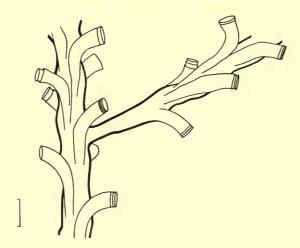


Fig. 3. Grammaria abietina. Part of colony, Trondheim Fjord, Norway (1912.12.21.599). Scale = $500 \mu m$.

NE of Shetland Isles, 61°35′ N, 0°47′ E ('Goldseeker' sta. 10), 204 m, 3 Sept. 1908, two fragments of hydrocauli on microslide, via J. Ritchie coll., 1964.8.7.61 (mentioned, Rees & Thursfield, 1965: 85). Other areas: Barents Sea, 'Vitiaz' sta. 523, 110 m, 16 Aug. 1950, large colony in spirit, Leningrad Academy of Sciences Zoological Museum, and microslide donated to British Museum (Natural History), 1975.7.11.1 (mentioned as G. stentor Allman, Naumov, 1960: 283; 1969: 306; see Remarks). Near Falkland Islands, 51°35′ S, 65°39′ W, 130 m ('Challenger' sta. 314), 21 Jan. 1876, two branched fragments of colonies plus one microslide, coll. H.M.S. 'Challenger', 1888.11.13.36 (syntypes of Grammaria magellanica Allman, 1888). Royal Sound, Kerguelen Island, 49°28′ S, 70°13′ E, 37–110 m ('Challenger' sta. 149D), 20 Jan. 1874, fragments of colonies in spirit plus one microslide, coll. H.M.S. 'Challenger', 1888.11.13.35 (syntypes of Grammaria stentor Allman, 1888). Off Marion Island, S Indian Ocean, 46°43′ S, 38°04′ E, 90–135 m ('Challenger' sta. 145), 27 Dec. 1873, colony and fragments in spirit plus one microslide, coll. H.M.S. 'Challenger', 1888.11.13.37 (syntypes of Grammaria insignis Allman, 1888).

Description. Colony erect, main stem and branches polysiphonic, branching irregular or imperfectly pinnate, branches tapering near the base. Hydrothecae long, tubular, variably outward-curving; rims even, circular, often renovated, frequently slightly flared; no apparent junction with pedicel; arranged in 4–8 longitudinal rows with hydrothecae of adjacent rows alternate; if 4 rows, hydrothecae often in decussate pairs. Hydranth yellow (Hincks, 1868), extensible roughly one hydrotheca-length beyond aperture; widest distally, hypostome conical, 18–20 tentacles held alternately elevated and depressed. Gonothecae borne in hermaphrodite coppiniae 'arranged on branches in small muffs. Surface of coppinia smooth owing to dense arrangement of the sterile tubes, their inwardly-curved ends forming a thick protective tangle above the gonothecal mouths' (Naumov, 1969).

MEASUREMENTS. See Table 2.

TABLE 2

Grammaria abietina. Measurements in µm

· Hydrotheca	North Sea (1964.8.7.61)	Trondheim Fjord (1912.12.21.599)	Nr Bergen, Norway (1962.10.7.23)
Diameter at rim COPPINIA	240-280	280-360	280-490
Overall length	_		3000
Overall width	_		1500
Diameter of sterile tubes	-	_	90-130

Variation. There are normally 4, 5 or 6 rows of hydrothecae on a hydrocaulus, and 8 rows have been recorded (Vervoort, 1972, as G. magellanica). When in 4 rows the hydrothecae are in opposite or almost opposite pairs. The hydrothecal rim is flared in some specimens and straight in others, this character having apparently no systematic value. The degree of outward curving of the hydrothecae varies, so that the plane of the hydrothecal aperture is parallel with the axis of the hydrocaulus in some specimens, while in specimens with shorter hydrothecae the plane of the aperture makes an angle of about 45° with the axis, and this character may vary even within a colony (Fig. 3).

Reproductive season. Little information. Fertile specimen taken near Bergen, Norway, 9 Apr. 1962 (1962.10.7.23).

DISTRIBUTION. Widely distributed in sub-arctic and arctic areas (Broch, 1918), extending south to much of the North Sea and some Danish waters. There seems to be no valid record from western coasts south of the Shetlands. Southerly records include Northumberland (Hincks, 1868; present material), Skagerrak (Kramp, 1935) and Oslo Fjord (Christiansen, 1972). A record from the north coast of France (Billard, 1904, repeated in Broch, 1918) is probably erroneous (see p. 381) and the statement of Christiansen (1972) that the species occurs on that coast lacks evidence. The weight of published opinion is that the species is absent from the English Channel and southern North Sea (Hincks, 1868; Hartlaub, 1895; Broch, 1927; Vervoort, 1946, 1949; Leloup, 1952; Hamond, 1957; Marine Biological Association, 1957; Teissier, 1965; Robins, 1969).

HABITAT. Published records indicate that the normal depth-range of this species is approximately 50–1500 m in boreal waters, rising to 10–250 m in arctic regions (Linko, 1911; Naumov, 1960, 1969; Christiansen, 1972). The species has been recorded on both silty and rocky substrates (Naumov, 1960, 1969; Calder, 1970).

Remarks. There seems no doubt from the original description of *Grammaria ramosa* Alder, 1856, that it should be regarded as a junior synonym of the present species and examination of the type series confirms that they are conspecific.

Vervoort (1972) has expressed doubt as to the distinctiveness of the three species erected by Allman (1888), *Grammaria insignis*, *G. magellanica* and *G. stentor*, and following examination of the type material they are here referred to the present

species. The characters on which they were based were differences in the branching of the colony and of the number of rows of hydrothecae, and whether or not the hydrothecal rim was flared. These characters are now known to be variable in G.

abietina and the three species proposed by Allman appear invalid.

The material assigned to *G. stentor* Allman, 1888, by Linko (1911) and Naumov (1960, 1969, examined here) has hydrothecae longer than in *G. abietina* as here defined, and may represent a distinct species. If so, a new name will have to be provided. *G. stentor* sensu Hartlaub, 1905, and Jaderholm, 1905, fall within the proposed limits of *G. abietina*. Jaderholm examined the type material of *G. intermedia* Pfeffer, 1889, and referred it to his own concept of *G. stentor*. His account suggests that *G. intermedia* also should be referred to *G. abietina*.

G. abietina var brevicyatha Broch, 1818, was distinguished on the basis of short, slightly out-turned hydrothecae, but such variation seems normal for the species

and no distinct variety need be recognized.

The material from Cherbourg, N France, referred to the present species by Billard (1904:164) is here identified as *Filellum serpens* (see p. 381).

Genus LAFOEA Lamouroux, 1821

Sertularia: Fleming, 1820:83 (part).

Lafoea Lamouroux, 1821:8; Hincks, 1868:198 (part); Naumov, 1960:272; Naumov, 1969:295.

NOMENCLATURE. The genus was named after an amateur botanist, Professor de Lafoye, of the University of Caen (Lamouroux, 1821; Lamouroux, Saint-Vincent & Deslongchamps, 1824).

Type species and material. Lafoea cornuta Lamouroux, 1821:8, pl. 65, figs 12-14 (by monotypy); $44-44\frac{1}{2}$ ° N, 52-53° W, 55-60 m; branched colony 100 mm long, coll. Capt. Laporte (Lamouroux, 1821); Botanical Institute collections, Caen. Specimen destroyed by bomb, 7 July 1944 (Redier, 1967).

DIAGNOSIS. Colony either stoloniferous or with stolons united to form erect polysiphonic hydrocauli with monosiphonic terminal branches. Hydrothecae lacking both operculum and diaphragm; tubular or bell-shaped, sometimes bent and thus bilaterally symmetrical; rim even, circular, sometimes flared; renovations frequent; pedicel twisted if present; gonothecae borne in hermaphrodite coppiniae.

REMARKS. Billard (1909: 311) examined the genotype material and referred the type species *L. cornuta* Lamouroux, 1821, to *L. dumosa* (Fleming, 1820), supporting the suggestion of Hincks (1868: 199) that the two are conspecific.

Lafoea dumosa (Fleming, 1820)

(Fig. 4)

Sertularia dumosa Fleming, 1820: 83-84.

Lafoea cornuta Lamouroux, 1821: 8, pl. 65, figs 12-14.

Campanularia dumosa: Fleming, 1828:548-549; Johnston, 1832:254, pl. 11, fig. 11; Johnston, 1838:157, pl. 23, figs 2-5; Johnston, 1847:113-115, pl. 27, figs 2-5, text-figs 20-21.

Capsularia dumosa: Gray, 1848:88.

Campanularia fruticosa Sars, 1850: 138-139; (syn. nov.). Campanularia gracillima Alder, 1856: 361, pl. 14, figs 5-6.

Lafoea dumosa: Hincks, 1868: 200-201, pl. 41, fig. 1, 1a (? syn. L. cornuta Lamouroux); Nutting, 1899: 747-751, pl. 64; Rufford, 1902: 62; Billard, 1909: 311 (syn. L. cornuta Lamouroux); Broch, 1918: 7-9; Totton, 1930: 158, fig. 14; Kramp, 1935: 123-124, figs 52a, 53; Fraser, 1944: 221-222, pls 45-46, fig. 205a-e; Ralph, 1958: 310; Rees & Thursfield, 1965: 79-80; Teissier, 1965: 19; Calder, 1970: 1524, pl. 5, fig. 3.

Lafoea fruticosa: Hincks, 1868: 202-203, pl. 41, figs 2, 2a-b (syn. C. gracillima Alder); Broch, 1918: 12-15 (syn. L. pocillum Hincks); Totton, 1930: 157-158, fig. 13; Kramp, 1935: 124-125, fig. 52c-d (syn. L. pocillum Hincks); Fraser, 1944: 223-224, pl. 46, fig. 206; Hodgson, 1950: 11; Naumov, 1960: 275-276, fig. 164; Millard, 1964: 13-14, fig. 3a-f; Rees & Thursfield, 1965: 80 (syn. L. pocillum Hincks); Millard, 1967: 175-176, fig. 2c; Naumov, 1969: 297-298, fig. 164; Calder, 1970: 1524-1525, pl. 5, fig. 4; Vervoort, 1972: 66-74, figs 19-21 (syn. L. gracillima Alder).

Lafoea pocillum Hincks, 1868: 204, pl. 40, fig. 2; Hincks, 1874b: 147; Crawford, 1895: 260; Rufford, 1902: 62; Linko, 1911: 114-116, fig. 20; Naumov, 1960: 273-274, fig. 161 (syn. Campanularia parvula Hincks); Naumov, 1969: 295-296, fig. 161 (syn. C. parvula Hincks).

Hebella pocillum: Ritchie, 1911: 33.

Lafoea gracillima: Broch, 1918:9-11; Totton, 1930:158-159, fig. 15a-b; Kramp, 1935: 125, fig. 526; Fraser, 1944:224-225, pl. 46, fig. 207; Ralph, 1958:310, figs 1y, 2a-c; Rees & Thursfield, 1965:80-81; Teissier, 1965:20; Calder, 1970:1525, pl. 5, fig. 5.

Lafoea fruticosa forma pocillum: Vervoort, 1949:148-149.

Type Material. Arbroath, Angus, Scotland, 1809; location of specimens unknown.

MATERIAL EXAMINED. Brattholmen, Hieltefjord, nr Bergen, Norway, 40-90 m. 9 Apr. 1962, part of a colony on microslide, coll. W. J. Rees, 1962.10.7.22 (Fig. 4). Kosterfjord, Sweden, 58°50′ N, 11°00′ E, 80-100 m, 23 Sep. 1964, hydrocaulus on microslide, coll. W. J. Rees, 1965.1.14.73. Väderö Islands, Sweden, 58°05' N, 11°04' E, 80 m, 1 Oct. 1964, several colonies in spirit, coll. W. J. Rees, 1965.1.14.136 and 1966.1.4.65. Löken, Gåsö Ranna, Gullmarfjord, Sweden, 25-30 m, 14 May 1959, two fertile colonies on Abietinaria sp., in spirit, coll. W. J. Rees, 1959.6.11.36. Gåsö, Gullmarfjord, Sweden, 20-30 m, 27 Aug. 1962, hydrocaulus on microslide, coll. W. J. Rees, 1962.11.8.13. Off Balta, Shetland Isles, Scotland, 100 m, colony in spirit, coll. A. M. Norman, 1912.12.21.237. Oban, Argyll, Scotland, two hydrocauli on microslide and colony on herbarium sheet, coll. T. Hincks, 1899.5.1.160, 216. Oban, Argyll, Scotland, infertile colony on Phycodrys rubens (L.) Batt., 5 in spirit, 1899.5.1.162 (holotype of Lafoea pocillum Hincks, 1868). Off Millport, Great Cumbrae Island, Bute, Scotland, 40 m, 18 Sep. 1970, four colonies in spirit, coll. C. Edwards, 1971.5.11.31. Berwick Bay, Berwickshire, Scotland, and Northumberland, England, several colonies on four herbarium sheets, coll. G. Johnston, 1847.9.24.68, 69, 70, 71 (mentioned, Gray, 1848:88; ? Johnston, 1838: 157). 'Deep water, Northumberland' (label with specimen), colony on herbarium sheet, coll. J. Alder, Hancock Museum, Newcastle-upon-Tyne [paratype of

⁵ Det. J. M. Price.

⁴ Fleming (1820) based the original description on specimens from three Scottish localities: from refuse of oyster-boats, 'Newhaven', identified in a later work as being near Edinburgh (Fleming, 1828); 'Aberbrothick', now called Arbroath, Angus; and 'Zetland'. The first and last being relatively imprecise, the type locality is here restricted to Arbroath.

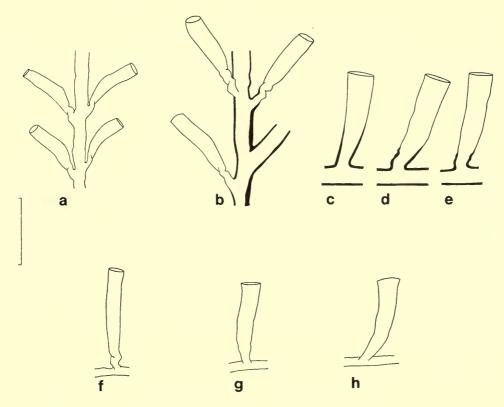


Fig. 4. a-e, Lafoea dumosa. a, part of colony, near Bergen, Norway, 40-90 m (1962.10.7.22); b, part of colony, east of Straits of Magellan, Argentina, 100 m (1890.4.11.2d); c-e, three adjacent hydrothecae, SW England (1959.9.17.108). f-h, three hydrothecae of holotype of Lafoea pocillum (1899.5.1.162), here referred to L. dumosa. Scale (a-h) = 500 μm.

Campanularia gracillima Alder, 1856; figured specimen, Alder, 1856: pl. 14, fig. 5 (J. B. Garfath, pers. comm.)]. Probably off Northumberland, 'in deep water' (Alder, 1856), colony in spirit, coll. J. Alder, 1857.8.3.51 [lectotype of Campanularia gracillima Alder, 1856 (Totton, 1930)]. Scarborough, Yorkshire, England, colonies on two herbarium sheets (one on Flustra sp.) coll. W. Bean, via G. Johnston coll., 1842.12.9.1, 1847.9.24.67 (mentioned, Gray, 1848: 88). North Sea, 60°02′N, 3°13′W, 160 m, 19 June 1906 ('Goldseeker' sta. 21a), two hydrocauli on microslide, coll. J. Ritchie, 1964.8.7.54 (mentioned, Rees & Thursfield, 1965: 80). North Sea, 59°21′N, 5°00′W, 125 m, 6 July 1906 ('Goldseeker' sta. 50), hydrocaulus on microslide, coll. J. Ritchie, 1964.8.7.50 (mentioned, Rees & Thursfield, 1965: 81). Plymouth, Devon, 8 Mar. 1898, hydrocauli on two microslides, coll. E. T. Browne, 1959.9.17.108, 114. Eddystone Ground, NW English Channel, 8 Mar. 1898, seven hydrocauli on microslide, coll. E. T. Browne, 1959.9.17.111. Eddystone ground, NW English Channel, 30 Mar. 1938, hydrocaulus on microslide, coll. W. J. Rees,

1969.12.2.45. Probably British, two colonies on herbarium sheets, coll. G. Johnston,

1847.9.24.69, 72 (mentioned, Gray, 1848:88).

Davis Strait, Greenland, 66°59′ N, 55°27′ W, 120 m, fragments of hydrocaulus on microslide, coll. H.M.S. 'Valorous', 1878.3.26.3. E of Str. of Magellan, Argentina, 52°20′ S, 67°39′ W, 100 m, 20 Jan. 1876 ('Challenger' sta. 313), part of colony on microslide, coll. H.M.S. 'Challenger', 1890.4.11.2d (Fig. 4). Off Oates Land, Antarctic mainland, 69°43′ S, 163°24′ E, 329–366 m, 22 Feb. 1911 ('Terra Nova' sta. 194), spirit material and two microslides, coll. British Antarctic ('Terra Nova') Expedition, 1929.10.28.64 (mentioned, Totton, 1930: 158).

Description. Colonies stoloniferous or erect. Stoloniferous colonies comprise irregularly-branched monosiphonic hydrorhizae with hydrothecae borne at irregular intervals. Erect colonies consist of polysiphonic hydrocauli, loosely and irregularly branched, arising from a straggling stolon network. Component perisarc tubes of erect colonies parallel, each bearing hydrothecae at irregular intervals giving bristly appearance. Hydrothecae long, tubular, even-rimmed, variably tapered below, sometimes asymmetrically; pedicel more or less well defined, usually kinked, but sometimes lacking so that hydrotheca is sessile. Form of hydrothecal pedicel usually constant within a colony. Hydranth long, retractile, c. 20 tentacles held alternately elevated and depressed (Kramp, 1935), hypostome conical. Hydranth and coenosarc often yellow. Gonothecae in hermaphrodite coppiniae.

MEASUREMENTS. See Table 3.

TABLE 3

Lafoea dumosa. Measurements in µm

•			•	
W English	W Sweden	N SCOTLAND	W SCOTLAND	W SCOTLAND
CHANNEL	(1965.1.14.73)	(1964.8.7.50)	(1899.5.1.160)	(1899.5.1.162)
(1969.12.2.45)				(holotype of
				Lafoea pocillum)
500-650	485-510	770-830	380-550	120-350
150-220	100	150-210	120-140	90-190
О	100-150	50	140-170	80-170
	CHANNEL (1969.12.2.45) 500-650 150-220	CHANNEL (1965.1.14.73) (1969.12.2.45) 500-650	CHANNEL (1965.1.14.73) (1964.8.7.50) (1969.12.2.45) 500-650	CHANNEL (1965.I.14.73) (1964.8.7.50) (1899.5.I.160) (1969.12.2.45) 500-650

Variation. The hydrothecal pedicel varies in length between colonies (see Remarks) and the degree of bilateral symmetry of the hydrothecae varies also. Neither character appears to be of systematic importance. Specimens from deep water have fewer hydrothecae per unit length of stolon, but within continental shelf depths this character seems constant. The so-called pedicel of the present species grades into the base of the hydrotheca. Although a pedicel is readily discernible if long, shorter pedicels are less distinct and it is possible to arrange specimens in a series in which the pedicel becomes progressively less distinct and is finally absent (Fig. 4). In each colony the range of pedicel length is small, but pedicellate hydrothecae can be found in colonies largely lacking pedicels, and sessile hydrothecae occur in predominantly pedicellate colonies.

REPRODUCTIVE SEASON. Fertile specimens recorded August in NW France (Teissier, 1965), 14 May 1959 in W Sweden (1959.6.11.36). The paucity of records suggests that in this species reproduction is usually vegetative.

DISTRIBUTION. Found throughout the area but apparently not common in the southern North Sea and eastern English Channel (Broch, 1918; Vervoort, 1946; Marine Biological Association, 1957; Teissier, 1965; Naumov, 1969), not having been found in a faunal survey off the coasts of Belgium (Leloup, 1952).

HABITAT. Occurs at all continental shelf depths, but not intertidally. On a wide variety of animal, plant and inert substrates, commonly on other hydroids; not on sand.

Remarks. The two nominal species *Lafoea fruticosa* (Sars, 1850) and *L. gracillima* (Alder, 1856) have been regarded as conspecific by some authors (e.g. Hincks, 1868; Hodgson, 1950; Naumov, 1960, 1969; Millard, 1967; Vervoort, 1972) and as valid species by others (e.g. Broch, 1918; Kramp, 1935; Fraser, 1944; Rees & Thursfield, 1965; Calder, 1970). Vervoort's detailed appraisal is particularly convincing and his view that the two are conspecific is accepted here.

In contrast, it appears that the distinctness of L. fruticosa from L. dumosa has been questioned only by Millard (1964), who described intermediate material. The two species have been distinguished by Hincks (1868) and apparently all subsequent authors (except Rufford, 1902, and Ralph, 19586) by the presence of a hydrothecal pedicel in L. fruticosa and its absence in L. dumosa which has been held to have sessile hydrothecae. However, the original description of L. dumosa (Fleming, 1820, repeated in Fleming, 1828) referred to 'nearly sessile' hydrothecae, implying that short pedicels were present. Johnston (1832) similarly mentioned 'nearly sessile' hydrothecae, stating that they 'can rarely be observed to be twisted at their insertions' as shown in his illustration. His later descriptions refer to 'nearly sessile' and 'almost sessile' hydrothecae (Johnston, 1838, 1847). Gray (1848) did not provide a description, but the ten colonies listed by him as L. dumosa and re-examined during the present work all have pedicellate hydrothecae. The material was from Johnston's collection, some being labelled Berwick Bay and probably, therefore, the Berwick Bay material described by Johnston (1832, 1838). Whether or not this is so it seems probable that Johnston, like Fleming, wished to imply that the pedicels were short, and not that they were absent. Further, in describing L. gracillima, Alder (1856) stated that the pedicels were 'longer' than in L. dumosa, indicating that he too considered L. dumosa to be pedicellate. Thus, when Hincks (1868) later gave specific status to specimens without pedicels and distinguished L. fruticosa as having them he was wrong to refer non-pedicellate material to L. dumosa and should have provided a new name. This seems never to have been done. It appears probable, however, that specimens lacking hydrothecal pedicels do not constitute a valid species and should nevertheless be referred to L. dumosa sensu Fleming, Johnston and Alder (op. cit.), L. fruticosa (Sars, 1851) and L. gracillima (Alder, 1856) falling within its synonymy.

⁶ In a key to the two taxa *L. dumosa* and *L. gracillima* Ralph separated them on the basis of short and long pedicels respectively, but she gave a description of *L. gracillima* only. Rufford ascribed a short pedicel to *L. dumosa* without comment.

The two nominal species Lafoea parvula (Hincks, 1853, as Campanularia) and L. pocillum Hincks, 1868, were thought to be conspecific by Naumov (1960, 1969). However, several authors (Broch, 1918; Kramp, 1935; Vervoort, 1949; Rees & Thursfield, 1965) have considered L. pocillum conspecific with L. dumosa (as L. fruticosa) and this opinion is supported by the present examination of the type material (Fig. 4). The material referred to Hebella pocillum (Hincks, 1868) by Fraser (1937, 1944) and Yamada (1955) is at present indeterminate; it may require a new specific name. The type material of L. parvula could not be located, but specimens labelled L. parvula (off Durham, England, coll. A. M. Norman, 1912.12.21.240) seemed identical with infertile colonies of Calicella syringa (Linnaeus, 1767) from which the hydrothecal operculae have been lost. It seems plausible that L. parvula was founded on such material.

Lafoea pygmaea Alder, in Hincks (1868: 205, pl. 40, fig. 3; type localities Tynemouth, Northumberland, and Sark, Channel Isles), was referred to Calicella in a later publication by Hincks [1874b:147 (footnote)]. This was accepted by Jaderholm (1909: 80), Bedot (1912: 315), Broch (1918: 9) and Stechow (1921: 228). However, Kramp (1935: 125) and Vervoort (1946: 199) regarded L. pygmaea as identical with L. gracillima (= L. dumosa), while Naumov (1960, 1969) referred it to L. pocillum (= L. dumosa). The type material in the Hancock Museum, Newcastle-upon-Tyne, and the description of Hincks (1868: pl. 40, figs 3, 3a-b), showing a well-demarcated pedicel with transverse annulations, are clearly of Calicella and it seems Hincks was justified in placing L. pygmaea in that genus (Cornelius & Garfath, in prep.). L. pygmaea was regarded as conspecific with C. syringa (Linnaeus, 1767) by Jaderholm (1909) and Broch (1918).

Family HALECIIDAE Hincks, 1868

DIAGNOSIS. Colonial Hydroida with short, cylindrical hydrothecae usually wider than deep; hydrothecal rims even, often flared, renovation common, desmocytes large, often birefringent. Hydrothecal pedicel often lacking. Hydranths larger than hydrothecae. Gonothecae usually sexually dimorphic. Sexual generation said to be a medusa in *Campalecium* Torrey, 1902 (Kossowska, 1911), eumedusoid in *Hydranthea* Hincks, 1868, and a sessile sporosac in *Halecium* Oken, 1815, and *Ophiodissa* Stechow, 1919.

Type genus. Halecium Oken, 1815.7

REMARKS. The nature of the sexual generation was shown by Rees (1957) to be a valid generic character in only some families among the athecate capitate hydroids. In the Haleciidae it appears to be correlated with other generic characters and is included here in the generic diagnoses. A similar correlation has been shown in certain genera of the Campanulariidae (Cornelius, 1975).

⁷ Oken's book was placed on the list of rejected works by the International Commission on Zoological Nomenclature (1956: Opinion 417), but application is currently being made to the Commission for validation of the name *Halecium* (see Cornelius, 1976).

The small birefringent bodies found inside the hydrothecal wall throughout this family (Fig. 11) and widely referred to as punctae (e.g. Vervoort, 1972) are probably desmocytes. They resemble those previously described in other classes of coelenterates, reviewed by Chapman (1969), but are much larger, being visible in some species at only 20 diameters' magnification. A preliminary account of their ultrastructure is to appear elsewhere. It is probable that the 'punctae' of the family Lafoeidae are also desmocytes. Present knowledge suggests that they have little systematic value at species level in either family, but comparative studies of their ultrastructure might prove differently.

Genus HALECIUM Oken, 18157

Halecium Oken, 1815:91; Johnston, 1847:58; Hincks, 1868:220; Fraser, 1944:183;Naumov, 1960:442.Thoa Lamouroux, 1816:210; Johnston, 1838:119.

Haloikema Bourne, 1890: 395.

Type species. Sertularia halecina Linnaeus, 1758 : 809 (Oken, 1815 : 91; Bedot, 1901 : 448).

DIAGNOSIS. Haleciidae with branched, erect colonies; lacking nematophores, large nematocysts, medusae and eumedusoid gonophores. Gonothecae usually sexually dimorphic.

REMARKS. Johnston (1847) drew attention to the seniority of *Halecium* to *Thoa* and his synonymy was followed by Hincks (1868) and all subsequent authors. *Haloikema* was first included in *Halecium* by Bedot (1911).

Halecium torreyi Kossowska, 1911, said by that author to release a medusa, was placed in the synonymy of Campalecium medusiferum Torrey, 1902, by Huvé (1954).

Halecium beanii (Johnston, 1938)

(Fig. 5)

Thoa beanii Johnston, 1838: 120-121, pl. 7, figs 1-2.

Halecium beanii: Johnston, 1847: 59-60, pl. 9, figs 1-2; Hincks, 1868: 224-225, pl. 43, figs 2, 2a-c; Vervoort, 1946: 161-163, figs 65-66; Ralph, 1958: 332-334, fig. 10a-b, e-k; Rees & Thursfield, 1965: 105-106.

Halecium scutum Clarke, 1876: 14–15, pl. 4, figs 13–14.

Halecium boreale Lorenz, 1886: 26-27, pl. 1, figs 1-2.

Halecium beanei Stechow, 1919: 33 (lapsus pro beanii).

Halecium beani: Naumov, 1960: 447-449, fig. 336 (syn. H. scutum Clarke; H. boreale Lorenz); Naumov, 1969: 483-484, fig. 336.

NOMENCLATURE. The species is named after W. Bean, who collected the holotype.

Type Material and locality. Holotype: Nr Scarborough, Yorkshire, England, in 'deep water', \$\varphi\$ colony 42 mm high on herbarium sheet, plus one microslide of \$\varphi\$ gonotheca from same colony, coll. W. Bean, 1847.9.18.181, 181a (Johnston, 1838, 1847).

⁷ See footnote on opposite page.

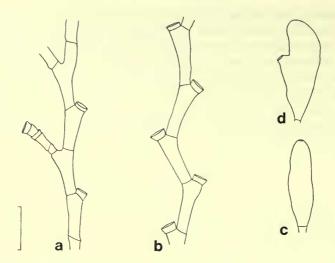


Fig. 5. Halecium beanii. a, part of colony, NE England (1956.2.2.27); b-c, part of colony and 3 gonotheca, Isle of Man (1959.10.17.8); d, φ gonotheca, near Bergen, Norway (1962.11.7.38). Scale (a-d) = 500 μ m.

OTHER MATERIAL EXAMINED. Bergen Fjord, Norway, 30–80 m, 1878, two colonies in spirit, coll. A. M. Norman, 1912.12.21.191. Espegrend, nr Bergen, Norway, 30 m, 9 Aug. 1962, \$\pi\$ colony on microslide, coll. W. J. Rees, 1962.11.7.38 (Fig. 5). NW of Bulbjerg, Denmark, 57° 12′ N, 8° 54′ E, 16 m, 3 Oct. 1922 ('Dana' sta. 2865), part of colony in spirit, coll. R. V. 'Dana', Copenhagen Zoological Museum (mentioned Kramp, 1935: 50, as *Halecium articulosum*).

Off Durham, England, Jul. 1874, colony in spirit, coll. A. M. Norman, 1912.12.21.186. Filey, Yorkshire, \(\phi\) colony in spirit, coll. T. Hincks, 1899.5.1.164. Bridlington Bay, Yorkshire, colony in spirit, coll. Ministry of Agriculture, Fisheries and Food, S.S. 'George Bligh', 1956.2.2.27 (Fig. 5). Sheerness, Kent, 10 Oct. 1892, one slide, coll. E. T. Browne, 1973.6.17.1. Weymouth Bay, Portland, Dorset, 20 m, several colonies in spirit, coll. R. Kirkpatrick, 1897.8.9.16. Berry Head, Brixham, Devon, 25 m, four \(\phi\) colonies in spirit, coll. R. Kirkpatrick, 1893.8.7.3, 1897.8.9.16. Eddystone ground, off Plymouth, Devon, 15 Sep. 1897, several \(\phi\) colonies on Chaetopterus tubes in spirit and one slide, coll. E. J. Allen, det. E. T. Browne, 1941.3.20.310. Plymouth, Devon, 1898, \(\phi\) colonies in spirit, coll. E. T. Browne, 1941.3.20.331. Isle of Man, 25 Mar. 1894, three colonies in spirit and one microslide (Fig. 5), coll. E. T. Browne, 1959.10.17.8.

DESCRIPTION. Colony erect, imperfectly pinnate, shrubby in habit. Main stem polysiphonic. Side-branches polysiphonic basally, component coenosarcs gradually branching off, final branches monosiphonic and usually flexuose; internodes equal, usually longer than broad, nodes oblique or transverse. Hydrothecae alternate, each on short hydrophore at distal end of internode; short, tubular, rim slightly flared, even. Usually 1-3 hydrothecal renovations, but up to 10 reported (Vervoort,

1972). Gonothecae on short pedicels below hydrothecae. 3 club-shaped, aperture terminal; 2 approximately bean-shaped, aperture tubular, in centre of concave side, c. 6 ova, 1 or 2 hydranths projecting through aperture.

MEASUREMENTS. See Table 4.

 $TABLE\ 4$ ${\it Halecium\ beanii.}\ \ Measurements\ in\ \mu m\ unless\ otherwise\ stated$

	U.S.S.R. (Naumov, 1969)	New Zealand (Ralph, 1958)	SW ENGLAND (1959.9.17.3)	SE ENGLAND (1973.6.17.1)
Hydrotheca		(1 , 55)	(-555-5-7-5)	(=5/5/6/-//-/
Length	50-70	6o	20-25	25-45
Breadth at rim	200-250	_	115-150	110-140
HYDROCAULUS DIAMETER	_	120-180	120-180	120-150
LENGTH OF INTERNODES	_	250-750	250-700	500-530
& GONOTHECA				
Length	Up to 2200	620-1000	700-850	_
Breadth (max.)	_	250	120-180	_
♀ Gonotheca				
Length	Up to 2200	1120-1125	_	1000-1200
Breath (max.)	_	310		430-480
MAXIMUM HEIGHT OF				'
COLONY	o·3 m	0·12 m	_	_

Variation. Hydrocauli of this species are variably flexuose; extremes are shown in Fig. 5.

REPRODUCTIVE SEASON. Fertile specimens recorded from S Devon, Norfolk and Roscoff, France, most months from January to October (Hamond, 1957; Marine Biological Association, 1957; Teissier, 1965).

DISTRIBUTION. Common throughout Britain and nearby seas. Apparently absent from the Baltic and rare in the Kattegat, commoner in the Skagerrak and Oslo Fjord (Broch, 1928; Christiansen, 1972).

Habitat. Rocky substrates; 5-100 m depth, occasionally deeper.

Halecium halecinum (Linnaeus, 1758)

(Fig. 6)

Corallina scruposa pennata, cauliculis crassiusculis rigidis Ray, 1724: 36.

Corallina erecta, tubulosa, pennata, halecis spinae facie Ellis, 1755: 17-19, pl. 10.

Sertularia halecina Linnaeus, 1758: 809.

Halecium halecinum: Oken, 1815:91; Johnston, 1847:58-59, pl. 8, figs 1-4; Hincks, 1868:221-223, pl. 42, figs a-d; Broch, 1918:36-38, fig. 11; Vervoort, 1946:158-161, figs 63-64; Leloup, 1952:140-141, fig. 74; Naumov, 1960:446-447, fig. 335, pl. 17, fig. 3; Naumov, 1969:482-483, fig. 335, pl. 17, fig. 3.

Thoa halecina: Johnston, 1838: 119-120, pl. 6, figs 1-4.

Halecium geniculatum Norman, 1867: 205; Hincks, 1868: 229; [non Halecium geniculatum Nutting, 1899 (= H. tenellum Hincks, 1861 (Naumov, 1960, 1969); see also synonymy of H. tenellum, p. 409)].

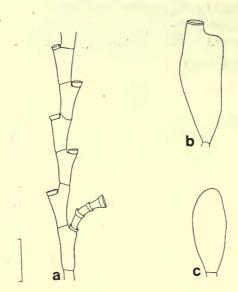


Fig. 6. Halecium halecinum. a-b, part of colony and ♀ gonotheca, Isle of Man (1959.9.17.5); c, 3 gonotheca, SW England (1898.5.7.86). Scale $(a-c) = 500 \mu m$.

TYPE MATERIAL AND LOCALITY. Whitstable, Kent, England, on shell of Ostrea edulis Linnaeus, 1758 (Ellis, 1755: pl. 10, figs A, a, B); location of specimens unknown.8

MATERIAL EXAMINED. Oban, Argyll, 1877, three colonies in spirit, coll. A. M. Norman, 1912.12.21.198. Bridlington Bay, Yorkshire, 7 Nov. 1921, several colonies in spirit, coll. S.S. 'George Bligh', 1956.2.2.26. S edge of Smith's Knoll, off Norfolk, 19 Jan. 1905, part of ♀ colony on microslide, coll. M.V. 'Goldseeker', det. J. Ritchie, 1964.8.7.273 (mentioned, Rees & Thursfield, 1965: 105). Isle of Man, 5 Jul. 1894, part of ♀ colony on microslide, coll. E. T. Browne, 1959.9.17.5 (Fig. 6). Menai Straits, Anglesey, Jul. 1964, part of 3 colony on microslide, coll. W. J. Rees, 1969.12.1.2. R. Deben estuary, Suffolk, several & colonies in spirit, coll. D. L. Serventy, 1933.7.1.12. East Solent, Hampshire, part of infertile colony on microslide, coll. A. Dendy, 1886.10.4.6. Off Lulworth, Dorset, 7 m, fragments of

Although some of Ray's and Ellis' material was later incorporated in the Hans Sloane herbarium, now in the British Museum (Natural History), there is no indication that the specimens of H. halecinum [H.S. 150: 37 (R.H. 79); H.S. 114: 1 (12)] in the Sloane herbarium are theirs since they have no collector's

name or locality. They cannot, therefore, be identified as type material.

Some Ellis hydroid material, which might have included the originally illustrated specimens of H. halecinum, was until recently preserved in the Hunterian Museum of the Royal College of Surgeons of England. Unfortunately, the Ellis material was almost certainly destroyed by a bomb during the Second World War and no Halecium material survives (see Cornelius, 1975: 267, footnote, for details).

⁸ Linnaeus quoted the earlier designations of Ray (1724) and Ellis (1755) and probably saw no material himself since he did not give a locality. Although the collections of the Linnean Society of London include material labelled *H. halecinum* [catalogued 1298.7–8 by Savage (1945)], it was probably added to the collection after 1758. Furthermore, none of it is the species currently recognized under this name. The specimens comprise two fertile colonies of *H. beanii* (sheet 7) and a colony of Sertularella sp. (sheet 8).

3 colony on two microslides, coll. F. Beckford, 1889.7.27.7. Tor Bay, Devon, 1875, part of ♂ colony on microslide, coll. A. M. Norman, 1898.5.7.86 (Fig. 6). Start Point, Devon, 18 m, part of ♀ colony on microslide, coll. R. Kirkpatrick, 1893.8.7.4. Plymouth, Devon, 19 Dec. 1892, part of ♂ colony on microslide, coll. E. T. Browne, 1959.9.17.4. Manacle Rocks, Porthoustock, Lizard Peninsula, Cornwall, 18 m, 29 Aug. 1965, part of ♂ colony on microslide, coll. R. Davis, pres. R. C. Vernon, 1966.1.1.3.

Description. Colony stiffly erect, regularly pinnate, with second and some third order branching. Hydrocaulus and main branches polysiphonic basally, component perisarc tubes branching off successively in groups; final branches monosiphonic, straight or slightly flexuose. Internodes equal, with distal hydrophore. Hydrothecae alternate, short, rim even, slightly flared, secondary, tertiary and some quaternary hydrothecae inside primary (Fig. 6) and longer than it. Hydranth larger than hydrotheca, hypostome conical, 17–22 tentacles. 3 gonotheca clubshaped, tapering basally, rounded distally; φ gonotheca oblong, tapering basally, subtruncate distally with lateral tubular aperture, 1–4 ova, with 1–3 hydranths projecting through aperture. Sexes on separate colonies.

MEASUREMENTS. See Table 5.

Table 5 $^{\prime}$ Halecium halecinum. Measurements in μm unless otherwise stated

	? U.S.S.R. (Naumov, 1969)	Netherlands (Vervoort, 1946)	SE ENGLAND (1964.8.7.273)	SW ENGLAND (1889.7.27.7)
Hydrotheca				
Length (diaphragm to rim)	90-150		20-40	25-40
Breadth at rim	170-210	100-200	140-165	130-145
Hydrocaulus diameter (min.)	_	_	190-225	100-150
Length of internodes		_	350-380	280-400
& GONOTHECA				
Length		800-1000	_	700-800
Breadth (max.)	_	c. 400		250-400
♀ Gonotheca				
Length	2000	1000-1300	1250-1400	
Breadth (max.)	500	400-500	350-600	
MAXIMUM HEIGHT OF COLONY	0·25 m	0·25 m		. —

REPRODUCTIVE SEASON. Fertile specimens recorded December to July in English Channel and off Norfolk (Hamond, 1957; Marine Biological Association, 1957; Teissier, 1965); one fertile & specimen 29 August, S Cornwall (1966.1.1.3).

DISTRIBUTION. Common throughout British Isles and adjacent continental shelf areas.

HABITAT. On stones, shells and other hard substrates, from sublittoral to edge of continental shelf and sometimes deeper (Broch, 1918). Detached fragments frequently occur on strand-line.

REMARKS. Halecium geniculatum Norman, 1867, appears from the original description to be conspecific with H. halecinum. The long, tubular hydrothecae described by Norman and regarded by him as diagnostic were probably just the renovated hydrophores which normally occur in H. halecinum.

Halecium labrosum Alder, 1859

(Fig. 7)

? Eudendrium pusillum Sars, 1857: 154, pl. 1, figs 14-16.

Halecium labrosum Alder, 1859: 354, pl. 13; Hincks, 1868: 225-226, pl. 44, fig. 1, text-fig. 27; Rees & Thursfield, 1965: 107-108 (syn. H. crenatum Hincks, 1874a); Naumov, 1969: 489-490, fig. 343; Calder, 1970: 1506-1508, pl. 1, figs 6-8.

Halecium pusillum: Kossowska, 1911: 347-350, figs 15-16; Broch, 1912: 16-17, fig. 2; Bedot, 1916: 115-116; [? non Teissier, 1965: 21; see Remarks].

Halecium annulatum Stechow, 1919: 33 (nom. nov. pro H. pusillum: Kossowska).

Halecium reflexum Stechow, 1919: 37-39, figs G-H; Teissier, 1965: 21.

Halecium undulatum Billard, 1921: 137-139, fig. 3; Leloup, 1952: 144-145, fig. 79; Hamond, 1957: 304-307, figs 12, 13 [syn. H. tenellum: Broch, 1918 (part); Kramp, 1929 (part); Kramp, 1932 (part); Kramp, 1938 (part)]; Hamond, 1963: 667; Calder, 1970: 1510-1512, pl. 2, figs 7-9; (syn. nov.).

Halecium tenellum: Fraser, 1944: 201-203, pl. 37, fig. 179 (part); Leloup, 1952: 144, fig. 77

(part).

Halecium schneideri: Leloup, 1952: 144, fig. 78 (? non H. schneideri Bonnevie, 1898).

Type material and localities. Syntypes: Large infertile colony on herbarium sheet and a fertile spirit specimen, probably male, in four pieces, both labelled 'deep water, Northumberland coast', Hancock Museum, Newcastle-upon-Tyne. Other type localities: Moray Firth and Shetland (Alder, 1859).

MATERIAL EXAMINED. Vatlestraumen channel, Hardanger Fjord, Norway, 60°20′ N, 5°12′ E, 15-25 m, 13 Apr. 1962, several colonies in spirit, three microslides of fragments (2 3, 1 sterile), coll. W. J. Rees, 1962.10.7.13 (Fig. 7), 35, 66. N Väderö Is., Skagerrak, 58°35' N, 11°04' E, 80 m, 1 Oct. 1964, colony in spirit and one microslide, coll. W. J. Rees, 1965.1.14.135 (Fig. 7). Firth of Lorn, Argyll, Scotland, 120-140 m, part of colony on microslide, coll. J. Murray, 1888.6.9.6. Mull of Kintyre, Argyll, Scotland, 90 m, two ♀ colonies in spirit and two microslides, coll. J. Murray, 1888.1.24.19 (Fig. 7). Plymouth, Devon, England, 17 Aug. 1898, six fragments of ♀ colonies on microslide, coll. E. T. Browne, 1959.9.17.9. Eddystone ground, western English Channel, 15 Sep. 1897, several fragments of colonies in spirit, coll. E. T. Browne, 1941.3.20.413. Eddystone ground, western English Channel, 19 Nov. 1897, parts of colonies on two microslides, coll. E. T. Browne, 1959.9.17.6, 123. Messina, Sicily, Italy, infertile colony on alga in spirit, holotype of Halecium pusillum Sars, 1857, Oslo Zoological Museum Cat. No. B1156 (mentioned, Broch, 1912; see Remarks, below).

DESCRIPTION. Colony erect, up to c. 50 mm, imperfectly pinnate, all but final branches polysiphonic; main branches slightly flexuose, side-branches inserted alternately with characteristic curve near base. Living tissues said to be purplish (Hincks, 1868). Internodes unequal, perisarc transversely wrinkled over much or

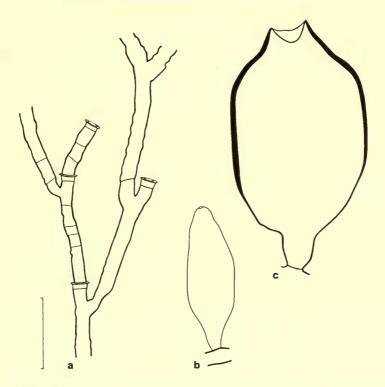


Fig. 7. Halecium labrosum. a, part of colony, Skagerrak, 80 m (1965.1.14.135); b, 3 gonotheca, near Bergen, Norway, 15–25 m (1962.10.7.13); c, 2 gonotheca, W Scotland, 90 m (1888.1.24.19). Scale (a–c) = 500 μ m.

all of length or, occasionally, smooth. Hydrothecae sessile, borne on prominent hydrophores, short, rims strongly recurved; up to c. 12 renovations common. Gonothecae on 1- or 2-ringed pedicel; gonothecal hydranths absent; δ ovate to linear, tapering basally and sometimes distally also, aperture simple, terminal; φ ovate, larger than δ , aperture simple, terminal; sexes on separate colonies.

MEASUREMENTS. See Table 6.

REPRODUCTIVE SEASON. Incompletely known. Fertile specimens recorded early May in southern North Sea, late May in Orkneys and Faroes, late June in Iceland (Hamond, 1957); 17 August 1898 at Plymouth (present material); September at Roscoff (Teissier, 1965).

DISTRIBUTION. A northern species known from localities throughout British coastal waters (Hincks, 1868; Hamond, 1957; Marine Biological Association, 1957). Although recorded from Roscoff, NW France (Teissier, 1965), the species appears absent from the Scilly Isles, Channel Islands, Belgium and Holland (Vervoort, 1946, 1949; Leloup, 1952; Robins, 1969) and the English Channel is probably near its southern limit. The species is known from the Danish coast and the Skagerrak (Kramp, 1935) but has been reported absent from the Baltic (Broch, 1928).

TABLE 6 Halecium labrosum. Measurements in um

14	W English Channel (1959.9.17.123)	PLYMOUTH (1959.9.17.9)	ARGYLL, SCOTLAND (1888.1.24.19)	W Norway (1962.10.7.13)
Hydrotheca				
Length (diaphragm to rim)	30-50	30-45	40-50	30-45
				(one 60)
Breadth at rim	240-280	150-165	220-255	140-155
				(one 170)
Hydrocaulus diameter (min.)	160-200	90-110	130-150	90-110
Length of internodes	950-1175	800-1700	550-700	600-820
& GONOTHECA				
Length		_	_	700-1000
Breadth (max.)	Marado-M	-		300-900
♀ Gonotheca				
Length	timeters.	640-1100	1350-1580	
Breadth (max.)	_	470-530	950-1090	_

HABITAT. Offshore, 5-200 m; found epizoic on exoskeletons of various invertebrates (Hamond, 1957) and probably occurs also on inanimate substrates.

REMARKS. The variation in transverse wrinkling of the internodal perisarc in this species has caused systematic confusion. As noted by Hamond (1957), specimens with completely smooth internodes have probably been confused with H. tenellum Hincks, 1861, which is, however, smaller in all dimensions, seldom has a wrinkled perisarc and lacks the curvature of the bases of the hydrocladia typical of H. labrosum.

Eudendrium pusillum Sars, 1857, type locality northern Sicily, remains problematical. It was recognized as Halecium by Kossowska (1911) who wrongly included H. lankesteri in its synonymy. Broch (1912) redescribed and figured part of the holotype and regarded the species as valid. The type material, re-examined here, has a recurved hydrothecal rim, a feature noted by Broch but not by Sars, and this and the curving bases of the branches are reminiscent of the present species. However, identification is made difficult by the type material being sterile and stunted in comparison with colonies of *H. labrosum*. It is not, therefore, possible to identify it confidently with the present species, which in addition has not been recorded so far south. Possibly the material from NW France identified as H. pusillum by Teissier (1965) was in fact H. labrosum as defined here; his is apparently the only suggestion that H. pusillum occurs in the present area.

Halecium reflexum Stechow, 1919, appears from the original description to resemble H. labrosum in its manner of branching, recurved hydrothecal rim and

wrinkled perisarc, and the two taxa appear conspecific.

Halecium undulatum Billard, 1921, seems to have been based merely on small colonies of H. labrosum. The two taxa appear similar in all characters except colony size and their distributions coincide so that there seems no reason to keep them distinct. Consequently the many H. tenellum records referred to H. undulatum by Hamond (1957) are identified here as H. labrosum. The gonothecae described by Calder (1970) under H. undulatum are similar to those of H. labrosum s. str.

The material described by Leloup (1947, 1952) under the name *H. schneideri* Bonnevie, 1898, is here referred to the present species. *H. schneideri* was a new name for *H. nanum* Alder, 1859, a species otherwise unrecorded from the present area. It was redescribed by Fraser (1944).

Halecium lankesteri (Bourne, 1890)

(Fig. 8)

Halecium robustum Pieper, 1884: 166–167; Babič, 1913: 470–473, figs 1–7; Bedot, 1914: 82; Stechow, 1919: 39–40; Teissier, 1965: 21; Fey, 1969: 397; [non Halecium robustum Verrill, 1873: 9; (= Zygophylax sp.; see p. 402)].

Haloikema lankesterii Bourne, 1890: 395-396, pl. 26.

Halecium lankesteri: Bedot, 1911: 213-217, pl. 11, figs 1-5 (= H. sessile: Billard, 1904); Stechow, 1923: 88; Prenant & Teissier, 1924: 25; Broch, 1933: 16-17, fig. 3; Vervoort, 1949: 145; Hamond, 1957: 302-304, figs 9-10; Marine Biological Association, 1957: 46; Vervoort, 1959: 221-224, figs 3-5; Millard, 1968: 257-258, fig. 1.

Nomenclature. The species was named after Professor E. R. Lankester.

Type material and locality. Syntypes: Near Duke Rock Buoy, Plymouth Sound, Devon, England, May 1889, several infertile colonies in spirit, coll. G. C. Bourne, 1974.2.28.1. Remaining type material recorded from Jennycliff Bay, Plymouth Sound, May 1890, not located.

Other material examined (All BM(NH) material except types). Studland Bay, Dorset, England, 6-8 m, \bigcirc colonies on six microslides, coll. R. Kirkpatrick, pres. F. Beckford via A. M. Norman, 1890.7.22.5 (Fig. 8). Mewstone, off Wembury, Devon, infertile colony on *H. halecinum*, in spirit, coll. E. T. Browne, 1948.10.1.125 (Fig. 8). Plymouth, Devon, 15 Jul. 1898, infertile fragments on microslide, coll. E. T. Browne, 1959.9.17.1. Plymouth, Devon, 1892, several infertile colonies in spirit, coll. W. Garstang, pres. A. M. Norman, 1912.12.21.572. E of Duke Rock Buoy, Plymouth, on piece of wire, c. 10 m, 2 Jul. 1973, dense growth of \bigcirc colony in spirit and hydrocaulus on microslide, coll. P. F. S. Cornelius, 1974.3.1.1 (Fig. 8; duplicate spirit material deposited in the Museum of the Marine Biological Association, Plymouth).

Description. Colony erect, up to c. 80 mm, usually unbranched but sometimes imperfectly pinnate; monosiphonic. Internodes often irregular in length, o-10 (usually 1) annulations between hydrothecae; bases of hydrocladia often curved inwards sharply. Hydrotheca on prominent hydrophore at distal end of internode; usually alternate; slightly tapering basally, short; rim not flared; up to c. 5 hydrothecal renovations. Hydranth large, 10–20 tentacles. Gonotheca on short pedicel below a hydrotheca. δ cylindrical, aperture terminal; φ kidney-shaped with tubular aperture in centre of concave side, 3–20 ova, 1–2 protruding polyps. Vervoort (1959) records sexes on separate colonies, δ gonothecae 'exclusively on renovated hydrophores' over entire colonies, φ on lower parts of colonies on secondary or tertiary hydrophores.

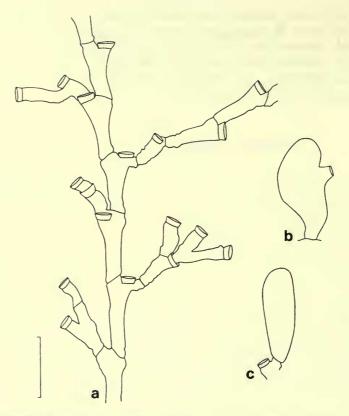


Fig. 8. Halecium lankesteri. a, part of colony, SW England (1948.10.1.125); b, Q gonotheca, SW England, 6–8 m (1890.7.22.5); c, δ gonotheca, SW England, c. 10 m (1974.3.1.1). Scale (a-c) = 500 μm.

MEASUREMENTS. See Table 7.

Variation. Hydrocladia may or may not appear to be sharply incurved basally, and Fig. 8 shows a specimen with both conditions. There may be o-10 internodal annulations between hydrothecae, and successive internodes are not identical in shape or length. The degree of wrinkling of the perisarc is variable. Tendril development occurs (e.g. 1974.3.1.1) but is unusual.

REPRODUCTIVE SEASON. June-July at Roscoff (Teissier, 1965); gonothecae of both sexes, Norfolk coast, 26 June 1952 (Hamond, 1957); & gonothecae, Plymouth, Devon, 2 July 1973 (1974.3.1.1). Infertile material from Plymouth includes the type specimens collected May 1889 and May 1890, and other material collected 15 July 1898 (1959.9.17.1).

DISTRIBUTION. There are published records from NW France, the Channel Islands, SW England, SW Wales and Norfolk (Bourne, 1890; Vervoort, 1949;

 $TABLE \ 7$ Halecium lankesteri. Measurements in μm unless otherwise stated

	SW ENGLAND (1974.2.28.1; type)	SW ENGLAND (1974.3.1.1)	GUINEA (Vervoort, 1959)	Mozambique (Millard, 1968)
Hydrotheca				
Length (diaphragm to rim)	45-70	30-35	20-25	30-40
Breadth at rim	200-230	130-140	120-130	140-150
Internodes				
Diameter (min.)	150	90-110		
Length	550-750	320-600	420-540	200-660
♂ Gonotheca				
Length		610-720	410-510	
Breadth (max.)		200	200-240	
♀ Gonotheca				
Length			88o	520-650
Breadth (max.)			450	380-450
MAXIMUM HEIGHT OF COLONY	c. 3 mm	c. 40 mm	c. 8 mm	c. 5 mm

Hamond, 1957; Teissier, 1965; Fey, 1969). The present records fall within this distribution and southern British waters appear to be the northern limit of this species. It does not appear to have been recorded from Ireland. The distribution abroad was summarized by Stechow (1923), Broch (1933), Vervoort (1959) and Millard (1968).

HABITAT. Recorded on stones (Bourne, 1890), other hydroids, crabs and Bryozoa (Hamond, 1957; Vervoort, 1959; present material), and on algae (Teissier, 1965; Fey, 1969). o-c. 50 m depth; not recorded intertidally.

REMARKS. The most useful descriptions of this species are those of Bourne (1890), Bedot (1911), Broch (1933), Vervoort (1949, 1959), Hamond (1957) and Millard (1968).

The measurements of the type material given here appear high in comparison with those of the other measured material. There is, however, no doubt that the type material is referable to the concept of the species both as first described by Bourne (1890) and as understood by recent authors (Hamond, 1957; Vervoort, 1959; Millard, 1968). The type specimens lack a flared hydrothecal rim which might otherwise identify them as *H. labrosum* Alder, 1959. They resemble closely the illustrations of Bedot (1911).

Although the hydranths of the type specimens were brown (Bourne, 1890), colourless and green hydranths have been recorded (Vervoort, 1949) and hydranth colour cannot be regarded as a useful specific character.

The confusion between *Halecium lankesteri* and the several species to which the combination *Halecium robustum* has been applied was summarized by Hamond (1957). The earliest usage, *H. robustum* Verrill, 1873, referred to a species of

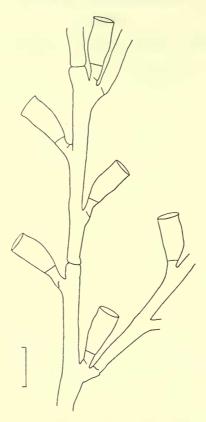


Fig. 9. Part of neotype of $Halecium\ robustum\ Verrill,\ 1873$, Massachusetts (Yale Peabody Museum No. 9137). Scale = 500 μm . The specimen is here referred to the genus $Zygophylax.^9$

Zygophylax so that the name robustum is not available for a Halecium species. H. lankesteri (Bourne, 1890) is the next available name for the present species.

Halecium muricatum (Ellis & Solander, 1786) (Fig. 10)

Sertularia echinata Linnaeus, 1761: 541 (part); Pallas, 1766: 152 (part); Linnaeus, 1767: 1310 (part).

Sertularia muricata Ellis & Solander, 1786: 59-60, pl. 7, figs 3-4.

⁹ The holotype of the nominal species *Halecium robustum* Verrill (1873:9; 786 m, St George's Bank, E Canada, 15 Sep. 1872, Yale Peabody Museum No. 3651) was never illustrated and is now lost (W. D. Hartman, pers. comm.) but a non-type specimen, labelled *H. robustum* in Verrill's hand, is extant and is here made neotype of *H. robustum* (off Cape Ann, Massachusetts, 17 Sep. 1878, branched hydrocaulus on microsclide, YPM No. 9137). The specimen (Fig. 9) has the characters of *Zygophylax* sensu Totton (1930). Thus the specific name *robustum* is not available for a *Halecium* species; and the species described by Verrill should be known as *Zygophylax robustum*. It predates other species of *Zygophylax*, but as specific limits within that genus are at present unclear no new synonymy is proposed. However, it may be noted that in lacking nematothecae and in having campanulate, straight or only slightly curved hydrothecae the neotype specimen resembles closely the original illustrations of *Z. pinnata* (Sars, 1874).

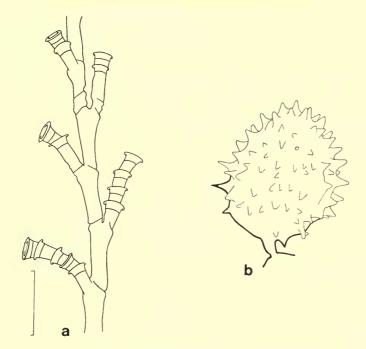


Fig. 10. Halecium muricatum. a, part of colony, E Scotland, 55 m (1969.12.5.9); b, \mathcal{Q} gonotheca (identified from contents; \mathcal{J} is externally similar), E Scotland, 20 m (1964.8.7.87). Scale (a-b) = 500 μ m.

Halecium filiforme Alder, 1862a: 315 (part); Alder, 1862b: 236 (part); Hincks, 1868: 228 (part).

Halecium muricatum: Hincks, 1868: 223-224, pl. 43, figs 1, 1a-b; Broch, 1918: 43-45, fig. 17; Fraser, 1944: 197-198, pl. 37, fig. 176; Vervoort, 1946: 163-164, fig. 67; Naumov, 1960: 456-457, fig. 347; Naumov, 1969: 492-493, fig. 347; Vervoort, 1972: 27, fig. 3b-d. Halecium murigatum Williams, 1954: 48 (lapsus pro muricatum).

Type locality and material. The original description was based on material supplied by a Dr David Skene of Aberdeen, but no locality was given and the specimen has not been located (see also footnote 8, p. 394). The type locality is here restricted to near Aberdeen, Scotland.

MATERIAL EXAMINED. Firth of Lorn, Argyll, Scotland, 130–150 m, part of infertile colony on microslide, coll. J. Ritchie, 1974.3.7.1. Off SE coast of Isle of Mull, Argyll, 10 Apr. 1971, two colonies in spirit, coll. P. F. S. Cornelius, 1971.5.11.30. Moray Firth, E Scotland, 55 m, 8 Dec. 1965, fertile fragments on two microslides, coll. F. W. E. Rowe, 1969.12.5.9 (Fig. 10). Burghead Bay, Moray Firth, 20 m, 22 Nov. 1905, fertile fragments on microslide, coll. J. Ritchie, 1964.8.7.87 (Fig. 10; mentioned, Rees & Thursfield, 1965: 109). Gullmarfjord, Sweden, 20–30 m, 27 Aug. 1962, fragment on microslide, coll. W. J. Rees, 1962.11.8.15. Probably W coast of Sweden, about 1758–60, 30 mm portion of fertile colony, Linnaeus colln., Linnean Society of London Catalogue No. 1298.14 (not type material; see Remarks).

Description. Colony erect, up to 100 mm, rarely 200 mm, imperfectly pinnate; main stem and larger branches polysiphonic; hydrocladia alternate. Nodes equally spaced, annulations often sloping alternately left and right but sometimes transverse. Hydrothecae alternate, on the monosiphonic branches, distal hydrophore usually demarcated by deep, irregular annulus; hydrotheca short, rim even, usually flared but sometimes straight; commonly up to c. 6 renovations. Gonothecae ovoid, pedicellate, with numerous 100–200 µm spines, in 9–15 rows. Sexes generally reported similar (see Remarks).

MEASUREMENTS. See Table 8.

 $\label{eq:table 8} Table \ 8$ $\textit{Halecium muricatum}. \ \ \text{Measurements in } \mu m$

	SE SCOTLAND	SW SCOTLAND	W Sweden
	(1964.8.7.87; Fig. 10)	(1974.3.7.1)	(1962.11.8.15)
Hydrotheca			
Length (diaphragm to rim)	30-80	35-50	40-60
Breadth at rim	130-160	140-170	240-280
Internode			
Length	480-600	600-800	850-1100
Minimum breadth	80-110	100-180	130-150
Gonotheca ($\delta = 9$)			
Length	1000-1500	-	
Breadth	900-1300	-	

REPRODUCTIVE SEASON. Little information. Fertile material recorded from Norfolk, 16 Nov. 1960 (Hamond, 1963) and in the British Museum (Natural History) collections from the Moray Firth, Scotland, 22 Nov. 1905 (1964.8.7.87) and 8 Dec. 1965 (1969.12.5.9). The apparent autumn breeding of this species in British waters is perhaps related to its northerly distribution. In Oslofjord specimens with gonothecae have been recorded in December and February and also in June (Christiansen, 1972) but it is not clear if the June material was living when collected.

DISTRIBUTION. An arctic and northern boreal species, extending south to the coasts of Scotland, NE England, Denmark and Sweden with occasional records in the central North Sea, Dogger Bank and off the Norfolk coast (Hincks, 1868; Broch, 1928; Kramp, 1935; Hamond, 1957, 1963; Rees & Rowe, 1969; Christiansen, 1972). Other records include SW Scotland (Vervoort, 1946; present material), Isle of Man (Bruce et al., 1966), Co. Antrim and Co. Down, Northern Ireland (Hincks, 1868; Stephens, 1905; Williams, 1954, in 1857). The species has not been included in recent faunal surveys of the following areas: Roscoff (Teissier, 1965), Scilly Isles (Robins, 1969), Plymouth (Marine Biological Association, 1957), Pembrokeshire (Crothers, 1966) and Anglesey (K. Hiscock, pers. comm.); and further eastwards was not reported from Belgium (Leloup, 1952), Holland (Vervoort, 1946) and the coast of Germany (Broch, 1927). There is apparently no record from the English Channel since Hincks (1868) recorded the species from Cornwall and South Devon, and no record this century from Irish waters.

Habitat. Mainly 10–200 m in Russian seas (Naumov, 1969), occurring down to 1350 m in the North Atlantic (Broch, 1918); not intertidal. Recorded on both hard substrates such as shells and rocks (Hincks, 1868) and on red algae (Christiansen,

1972).

REMARKS. The combination Sertularia echinata Linnaeus, 1761, was used in several works between 1761 and 1802 (Bedot, 1901), but the specific name was apparently not used between then and 1910 (Bedot, 1905, 1910, 1912, 1916, 1918, 1925) and has apparently not been used since. The taxon was tentatively referred to the present species by Johnston (1838:121; 1847:61) and later by Vervoort (1046:163) but it appears that this action was only partly correct. The type material of S. echinata is preserved in the collections of the Linnean Society of London, on herbarium sheet No. 1298.14 (Savage, 1945). The sheet bears two specimens. That on the left comprises two infertile colonies arising from a common substrate, each referable to Sertularia cupressina Linnaeus, 1758. That on the right, however, is a fertile fragment 30 mm long referable to H. muricatum as defined above. The original diagnosis of S. echinata was probably made from both the specimens, as it includes characters of both S. cupressina ('denticulis opposite obtusiusculis') and of H. muricatum ('calycibus [gonotheca] obovatis compressis reticulatis muricatis'). The specimen on the left of the sheet is here nominated as lectotype, so that the name S. echinata Linnaeus, 1761, falls into the synonymy of S. cupressina Linnaeus, 1758. The later descriptions of S. echinata provided by Pallas (1766) and Linnaeus (1767) perpetuated Linnaeus' (1761) confusion of the two species. The first available name for the present species is thus Sertularia muricata Ellis & Solander, 1786.

Halecium filiforme Alder, 1862a, was described only briefly by Alder without illustration (1862a, b) and the description was repeated by Hincks (1868). Hincks considered the species closest to 'H. plumosum' (= H. sessile; see p. 409) but quoted Alder as later regarding H. filiforme as 'probably a mere variety or an immature state of some other species'. The original description agrees with 'H. plumosum' in the following characters: hydrocaulus 'very slender, flexible', monosiphonic, little branched; length 115 mm ($4\frac{1}{2}$ inches); 'branchlets' arising from the side of a hydrotheca; and differs in that the hydrothecae are said to be 'rather slender, tubular, with a slightly everted margin'. The type material of H. filiforme in the Hancock Museum, Newcastle-upon-Tyne, is a mixed series comprising specimens referrable to both H. muricatum and H. sessile Norman, 1867. The herbarium specimen labelled 'Halecium filiforme, deep water, Northumberland' is here designated lectotype of H. filiforme. It is a large infertile colony of H. muricatum, of which name H. filiforme thus becomes a junior synonym. The Newcastle-upon-Tyne material will be more fully described elsewhere (Cornelius & Garfath, in prep).

Most authorities have considered the gonothecae of the two sexes identical (e.g. Hincks, 1868; Fraser, 1944; Vervoort, 1946), but Rees & Thursfield (1965: 109) implied that there is a difference without providing details of how they differ. The weight of opinion at present suggests that there is no difference,

however.

Halecium sessile Norman, 1867

(Fig. 11)

Halecium filiforme Alder, 1862a: 315 (part); Alder, 1862b: 236 (part); Hincks, 1868: 228

(part); (see p. 405).

Halecium sessile Norman, 1867: 205; Hincks, 1868: 229-230, pl. 44, fig. 2; Storm, 1882: 19 (? syn. H. plumosum); Billard, 1904: 52-53, 157-160; pl. 3, figs 8-9, pl. 6, figs 1-14; Kuhn, 1913: 139, fig. 58; Vervoort, 1941: 195-196; Ralph, 1958: 331-332, figs 9h-i, 10c-d; Teissier, 1965: 21; Vervoort, 1966: 100-102, fig. 1 (syn. H. kofoidi Torrey, 1902; H. lighti: Nutting, 1927); Christiansen, 1972: 298.

Halecium plumosum Hincks, 1868: 227-228, pl. 64, fig. 1; Kuhn, 1913: 70, 112, fig. 46;

Christiansen, 1972: 299; (syn. nov.).

Halecium articulosom Clarke, 1875: 63, pl. 10, fig. 6; Jaderholm, 1909: 58, pl. 5, fig. 7; Kramp, 1935: 149-150, fig. 62c; Kramp, 1938: 32; Fraser, 1944: 185-186, pl. 33, fig. 159; Leloup, 1952: 143-144, fig. 76; Christiansen, 1972: 299; (syn. nov.).

Type Material and locality. 'Deep water in the Minch', between Outer Hebrides and mainland Scotland; specimen not located.

MATERIAL EXAMINED.¹⁰ Gullmarfjord, W Sweden, c. 30 m, 13 Jan. 1910, colony in spirit, coll. T. Mortensen, Copenhagen Zoological Museum (CZM). Gullmarfjord, W Sweden, 15 Oct. 1918, colony in spirit with epizoic *Halecium beanii*, coll. Kristineberg Zoological Station, CZM. 22 km N of Hirtshals, Denmark, 110 m ('Thor' sta. 1576), 27 Jun. 1911, colony in spirit, CZM. Nr Fredriskhavn, Denmark, 17 m, 13 Aug. 1930, coll. P. L. Kramp, CZM. Oresund, Denmark, c. 25 m, 27 Aug. 1928, CZM.

Great Cumbrae Island, R. Clyde, W Scotland, 15-30 m, 18 May 1955, colony in spirit plus one microslide, coll. W. J. Rees, 1956.1.1.16. Salcombe, Devon, on Nemertesia sp., infertile colony in spirit, coll. T. Hincks, 1899.5.1.167. Near Eddystone Rock, off SW coast of England, 10 Sep. 1897, infertile colony in spirit and fragments on microslide, coll. E. T. Browne, 1941.3.20.414. 3 km E of Eddystone Rock, 6 Jul. 1971, two infertile colonies in spirit plus one microslide, coll. P. F. S. Cornelius, 1971.7.10.1. 4 km NNW of Eddystone Rock, c. 40 m, 20 Jul. 1972, infertile colony in spirit, coll. P. F. S. Cornelius, 1973.11.22.7. Bay of Biscay, 7 Mar. 1912, fragments of 3 colony on microslide, coll. E. T. Browne, 1959.9.17.8. Off R. Sado, Portugal, infertile colony in spirit, coll. W. Saville Kent, 1872.2.3.137. South of Terceira Island, Azores, 610 m, Aug. 1959, infertile colony and fragments on microslide, coll. Imperial College (University of London) Azores Expedition, 1962.1.15.12.11 Bay of Fundy, New Brunswick, Canada, 1872, 30 mm infertile colony in two parts, coll. U.S. Fisheries Commission (U.S.F.C.), Yale Peabody Museum (YPM) 3478. Casco Bay, Maine, U.S.A. 1873, five fragments of colonies (four infertile, one Ω), coll. U.S.F.C., YPM 5460 (syntypes of Halecium articulosum Clarke, 1875). Eastport, Maine, U.S.A. 1868, eight fragments of colonies (five infertile, three Ω), coll. A. E. Verrill, YPM 3663-4. Eastport, Maine, U.S.A. 1868, 40 mm colony, coll. A. E. Verrill & S. I. Smith, YPM 3477. Jervis Bay, New South Wales, Australia, c. 20 m, 1898, infertile fragment on microslide, coll.

 $^{^{10}}$ The Danish and Swedish material is that mentioned by Kramp (1935: 150) as *Halecium articulosum*. 11 The microslide specimen has an epizoic colony of *Lafoeina* sp., a genus not previously recorded from the Azores (Rees & White, 1966).

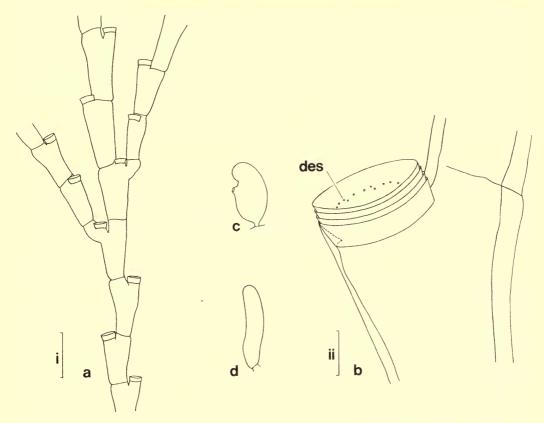


Fig. 11. Halecium sessile. a-b, part of colony and one hydrotheca, SW England (1971.7.10.1); c, \mathcal{Q} gonotheca, N France (redrawn after Billard, 1904: pl. 6, fig. 14); d, \mathcal{S} gonotheca, Bay of Biscay (1959.9.17.8). Scale i (a, c, d) = 500 μ m; scale ii (b) = 50 μ m. des. = desmocyte ('puncta').

H.M.S. 'Thetis', ex J. Ritchie collection, 1964.8.7.88 (mentioned, Rees & Thursfield, 1965: 109).

Description. Colonies monosiphonic, up to 50 mm, or polysiphonic up to 300 mm; all sizes branching, the larger colonies branching irregularly, and being limp when out of water. Hydrocaulus variably flexuose, nodal constrictions transverse or sloping in alternate directions. Internodes approximately equal, becoming shorter distally, widely variable in length to breadth ratio between colonies; hydrophore distal, long, usually parallel with internode but sometimes shorter and sloping outwards. Base of hydrotheca usually at approximately 90° to internodal axis although this angle may be greater; hydrotheca very reduced, walls straight, divergent, rim even, not flared; characteristic annulus of perisarc thickening below base of hydrothecal wall, wedge-shaped in optical section (Fig. 11). Hydrothecal renovation frequent, secondary hydrothecae usually forming directly on diaphragm resulting in very short hydrothecal chains (Fig. 11). Hydrocladia inserted

alternately, arising from sides of hydrophores, associated hydrotheca consequently axillary. Hydranth long, 18-25 tentacles (Vervoort, 1941); citron-yellow colour recorded (Storm, 1882) but this perhaps unusual. 3 gonotheca tubular, slightly curved, aperture terminal; 4 gonotheca kidney-shaped, with tubular aperture on concave side, similar to that of 4 beanii, with two projecting hydranths (Billard, 1964; Ralph, 1958).

MEASUREMENTS. See Table 9.

Table 9 ${\it Halecium~sessile}. \ \ {\it Measurements~in~} \mu m$

					New
	BAY OF	W English	NEW SOUTH		ZEALAND
	BISCAY	CHANNEL	WALES	Azores	(Ralph,
	(1959.9.17.8)	(1971.7.10.1)	(1964.8.7.88)	(1962.1.15.12)	1958)
Hydrotheca				,	,
Length (diaphragm to					
rim)	25-35	45-55	40-50	25-35	15-20*
Breadth at rim	130-170	160-185	150-170	120-150	c. 125
Internode					
Breadth (min.)	90-130	200	130-170		
Length	550-700	550-650	340-500		500-680
♂ Gonotheca					
Length	980-1035		**********		620-750
Breadth (max.)	185-220				210
♀ Gonotheca					
Length		******			750
Breadth (max.)					400
* D' 1 1 1					•

^{*} Rim to desmocytes ('punctae').

REPRODUCTIVE SEASON. August to end October in NW France (Teissier, 1965; Fey, 1969); possibly also June-July, Cherbourg (Billard, 1904). (The fertile Bay of Biscay material is dated 7 March 1912 in E. T. Browne's hand, but this may simply be the date on which he prepared the slide.)

DISTRIBUTION. Widespread in the North Atlantic including the whole of the British Isles, North Sea and English Channel (Hincks, 1868; Broch, 1918, Kramp, 1935) including the Skagerrak and Kattegat but not the Baltic (Broch, 1928; Kramp, 1935, as *H. articulosum*; Christiansen, 1972). Records are nevertheless scattered. As *H. sessile* the species has been recorded from the Hebrides (Norman, 1867; Hincks, 1868), Dorset and Devon (present material), Denmark (Kramp, 1935) and NW France (Teissier, 1965; Fey, 1969); and as *H. plumosum*, probably indicating records of larger colonies, from Aberdeen (Forbes, 1872), Firth of Forth (Leslie & Herdman, 1881), the Clyde (Chopin, 1894) and 'Ireland' (Hincks, 1868; Duerden, 1897).

HABITAT. Apparently all depths to edge of continental shelf. Recorded on algae and worm-tubes (Sabellaria sp.) (Billard, 1904).

REMARKS. This species was last redescribed by Ralph (1958).

The species Halecium filiforme Alder, 1862a, is discussed under H. muricatum

(p. 405).

Halecium plumosum Hincks, 1868, was tentatively identified with the present species by Storm (1882); Christiansen (1972) also commented on the similarity. The present material includes specimens referable to Hincks' description, but in their mode of branching, structure of hydrotheca, manner of hydrothecal renovation and possession of an annular thickening below the diaphragm they resemble specimens referable to H. sessile sensu Norman, i.e. smaller colonies. It seems that H. plumosum was founded merely on large colonies of the present species and is here regarded conspecific.

Halecium articulosum Clarke, 1875, can be reduced to a synonym of the present species. Of the type material only that from Casco Bay, Maine, could be located (W. D. Hartman, Yale Peabody Museum, pers. comm.). It agrees with H. sessile material in having very short chains of hydrothecae, in having the annular thickening below each hydrotheca, in having a hydrotheca axillary to each side-branch, in the shape of the female gonotheca and in general colony habit, so that it appears that

the two taxa are conspecific.

Most of the material assigned to *H. articulosum* by Kramp (1935:150) was examined and similarly found to be identical with *H. sessile*. Apparently the only other European records as *H. articulosum* are those of Jaderholm (1909), Vervoort (1942), Leloup (1952) and Christiansen (1972), respectively from W Sweden, N France, Belgium and Oslofjord. The Belgian material is well described, and is almost certainly *H. sessile*. The W Swedish, French and Oslofjord material, identified from the descriptions of Clarke (1875), Jaderholm (1909) and Kramp (1935), which are here referred to *H. sessile*, are also probably the present species.

Halecium lighti Hargitt, 1924, was referred to the present species by Vervoort (1941) who later, however, accepted the species as valid (Vervoort, 1966). Nutting

(1927) had previously doubted its validity.

Halecium tenellum Hincks, 1861

(Fig. 12)

Halecium tenellum Hincks, 1861: 252, pl. 6, figs 1-4; Hincks, 1868: 226-227, pl. 45, figs 1, 1a-c; Broch, 1912: 17-18, fig. 3; Broch, 1918: 46-50, fig. 20 (part); Kramp, 1935: 145-146, fig. 60A; Fraser, 1944: 201-203, pl. 37, fig. 179 (part); Vervoort, 1946: 164-165, fig. 68; Leloup, 1952: 144, fig. 77 (part); Hamond, 1957: 307, fig. 14; Millard, 1957: 193, fig. 5; Vervoort, 1959: 229-231, fig. 8; Naumov, 1960: 454, fig. 344 (syn. H. geniculatum Nutting, 1899); Millard, 1966a: 471, fig. 11; Vervoort, 1966: 102, fig. 2; Naumov, 1969: 490-491, fig. 344 (syn. H. geniculatum Nutting, 1899).

Halecium geniculatum Nutting, 1899: 744-745, pl. 63, figs 1a-d; [non H. geniculatum Norman,

1867 = H. halecinum (Linnaeus, 1758)].

Halecium washingtoni Nutting, 1901: 789 (nom. nov. pro H. geniculatum Nutting, 1899).

Type material and locality. Syntypes: Salcombe Bay, Devon, England, & colony, on *Cellaria fistulosa* (Linnaeus, 1758) (Bryozoa), in spirit plus three microslides, 1899.5.1.168 (Fig. 12).

¹² Syn. Salicornaria farciminioides: Hincks, 1861 (International Commission on Zoological Nomenclature, 1971: Opinion 949).

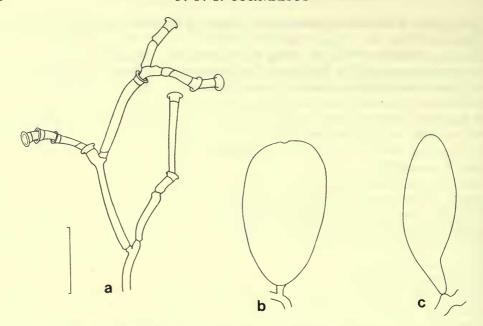


Fig. 12. Halecium tenellum. a, part of colony, SW England (syntype, 1899.5.1.168); b, \mathcal{P} gonotheca, Republic of South Africa, 46 m (redrawn after Millard, 1966a: fig. 11 E); c, \mathcal{P} gonotheca, McMurdo Bay, Antarctica (1964.8.7.90). Scale (a-c) = 500 μ m.

OTHER MATERIAL EXAMINED.¹³ Hardanger Fjord, Norway, 200 m, fragments in spirit, coll. A. M. Norman, 1912.12.21.208. Oban, Argyll, Scotland, 1877, several colonies on Diphasia rosacea (Linnaeus, 1758), coll. A. M. Norman, 1912.12.21.209. Monte Brazil West, Terceira Island, Azores, 20 m, Aug. 1959, fragments of colonies on sertularian hydroid, coll. Imperial College (University of London) Azores Expedition, 1962.1.15.24. Porto Santo Island, Madeira, 120 m, several colonies on Eudendrium sp., in spirit and microslide, coll. R. Kirkpatrick, 1919.8.14.7. Simon's Bay, Simon's Town, Republic of South Africa, 'shallow water', colonies on fragments of type of Halecium dichotomum Allman, 1888, two microslides, coll. H.M.S. 'Challenger', 1888.11.13.9B. False Bay, Republic of South Africa, several colonies in spirit, pres. South African Museum, sample of material mentioned by Millard, 1957: 193, station FAL 290C, BM(NH) 1957.4.26.18. Bay to east of Cape Royds, Antarctica, May 1908, 20-40 m, fragments on microslide, coll. Shackleton Antarctic Expedition, 1964.8.7.90 (mentioned, Rees & Thursfield, 1965:110). Off cable, McMurdo Bay, Antarctica, 17 Feb. 1904, on Halecium arboreum Allman, 1888, several colonies in spirit, coll. National Antarctic ('Discovery') Expedition, 1907.8.20.42 (mentioned, Hickson & Gravely, 1907: 28).

Description. Colony erect, up to 20 mm, delicate, monosiphonic, irregularly branched. Hydrocaulus zig-zag in general appearance, internodes usually straight

¹³ This section includes all material of this species in the British Museum (Natural History) collection except the type series.

and narrow, angle between them about 140°. Usually 1-3 annular wrinkles at each end of an internode, but some internodes wrinkled throughout, with intermediate conditions. Hydrotheca borne on prominent distal hydrophore, short, rim flared. 3 gonotheca pedicellate, ovoid, flattened in one plane; \$\phi\$ similar, slightly larger, no protruding hydranths (Millard, 1966a); sexes on separate colonies (Millard).

MEASUREMENTS. See Table 10.

 $\begin{tabular}{ll} TABLE \ IO \\ \end{tabular} \begin{tabular}{ll} Halecium \ tenellum. \ Measurements in μm unless otherwise stated \\ \end{tabular}$

	SW ENGLAND (syntypes)	South Africa (Millard, 1966a)	South Africa (Vervoort, 1966)	? U.S.S.R. (Naumov, 1969)		
Hydrotheca		,	,	,		
Length	25-30	_	30-65	40-80		
Breadth at rim	100-130	_	120-135	120-190		
Hydrocaulus diameter						
(min.)	50			_		
LENGTH OF INTERNODES	500-850	_	875-1300			
d Gonotheca						
Length	540-720	1070 (max.)	_	_		
Maximum breadth	200	600		_		
♀ Gonotheca						
Length	_	1070 (max.)	_			
Maximum breadth		510	_	_		
MAXIMUM HEIGHT OF COLONY	c. 5 mm	4 mm		15-20 mm		

REPRODUCTIVE SEASON. Not recorded.

DISTRIBUTION. Poorly known, as many published records are dubious (Hamond, 1957; see Remarks below). British material in the British Museum (Natural History) collection comes from only two localities, Salcombe, Devon (syntypes), and Oban, Argyll. However, the wide distribution suggested by apparently valid published records implies that the species occurs throughout British and nearby waters.

HABITAT. Frequently recorded on other thecate hydroids and on Bryozoa, occurring from sublittoral at least to 495 m (Vervoort, 1966). Recorded on Bryozoa by Hincks (1861, Cellaria fistulosa), Hamond (1963, Bugula plumosa) and Robins (1969, Cellaria sp.). Its apparent association with the hydroid Idiella pristis (Lamouroux, 1816) on the West African coast was considered by Vervoort (1959) simply to reflect substrate availability.

REMARKS. The small size and straight, smooth internodes of this species serve to distinguish infertile specimens from young specimens of *H. labrosum*. In addition the curving bases of the hydrocladia in *H. labrosum* contrast with the straighter bases in the present species. Published records should be treated with caution. A summary of records in which the species was confused with *H. labrosum* and its junior synonym *H. undulatum* Billard, 1921, was given by Hamond (1957). See also the Remarks section under *H. labrosum* (p. 398).

Genus HYDRANTHEA Hincks, 1868

Atractylis Wright, 1858: 447 (part); Hincks, 1862: 461.

Hydranthea Hincks, 1868: 99 [nom. nov. pro Atractylis Wright (part)].

Type species. Hydranthea margarica (Hincks, 1862), by monotypy.

DIAGNOSIS. Colony hydrorhizal; hydrotheca pedicellate, borne singly, too short to contain hydranths which are large; gonophore eumedusoid; large nematocysts present.

Hydranthea margarica (Hincks, 1862)

(Fig. 13)

Atractylis margarica Hincks, 1862: 461, pl. 9, figs 4, 4a-e, x; Hincks, 1863: 45-46.

Hydranthea margarica: Hincks, 1868: 100-101, pl. 19, figs 1, 1a-c; Marine Biological Association, 1957: 46; Huvé, 1954: 178-182, pls 3-6 (= Halecium billardii Kossowska); White, 1956: 39-41; Millard & Bouillon, 1973: 45-46, fig. 6a.

Halecium margaricum: Kossowska, 1911: 327-328, fig. 1.

Halecium billardii Kossowska, 1911: 328-331, figs 2-3.

Halecium billardii Kossowska, 1911: 328–331, figs 2–3. Halecium billardii var. exigum Kossowska, 1911: 331, fig. 4.

Type material and locality. Ilfracombe, Devon, England, on *Flustra foliacea* (Bryozoa), c. 20 m (Hincks, 1863); probably collected summer, 1861 (Hincks, 1862); present location unknown.

MATERIAL EXAMINED. Off Sanda Island, Argyll, Scotland, 20–30 m, on Flustra sp. (Bryozoa), colony in spirit and two microslides, coll. R. B. Pike, 1955.11.15.11 (mentioned, White, 1956). Off Oxwich Point, Gower Peninsula, Glamorgan, Wales, c. 20 m, 15 Jun. 1971, on Flustra sp., colony in spirit, coll. D. N. Huxtable, 1973.3.3.1. Off Poole, Dorset, England, c. 15 m, on Flustra sp., colony in spirit, coll. F. Beckford, 1889. 7.27.5. Outside Swanage Bay, Dorset, c. 20 m, on Flustra sp., colony in spirit, coll. R. Kirkpatrick, 1897.8.9.2. Plymouth, Devon, England, 24 Feb. 1914, colony in spirit, coll. E. T. Browne, 1954.8.3.42. Plymouth, 23 Oct. 1913, fertile colony on Halecium halecinum, in spirit and one microslide, coll. E. T. Browne, 1954.8.3.34. Stoke Point, Plymouth, 23 Oct. 1913, colony on fragments of gastropod shell, in spirit, coll. E. T. Browne, 1954.8.3.44. Roscoff, NW France, 12 Sep. 1956, colony on bivalve shell, in spirit, coll. W. J. Rees, 1956.10.24.1–2.

Description. Colony reptant, stolon bearing single hydranths at irregular intervals. Hydranths yellowish-white (Hincks, 1868), on short unringed pedicels, narrow at base, widest just below hypostome, 20–30 tentacles held alternately elevated and depressed (Hincks, 1868; Browne, in White, 1956), with small basal web. Hydrotheca short, walls slightly divergent, rim even, diaphragm domed downwards; c. 20 desmocytes ('punctae'). Large, conspicuous banana-shaped or straight nematocysts (microbasic euryteles, Huvé, 1954), 30–40 µm long, throughout tissues of hydranth and coenosarc, scattered or in clumps, particularly conspicuous on tentacular web. Gonophores on short pedicel tapering basally, attached to stolon; gonotheca short (Fig. 13) or absent; pedicel base said to be enclosed in small chitinous cup (Hincks, 1868) but this not present in all specimens (e.g. BM(NH)

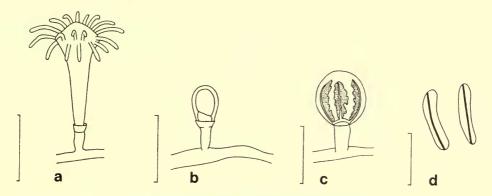


Fig. 13. Hydranthea margarica. a, reconstruction of hydranth and hydrotheca, W Scotland, 20-30 m (1955.11.15.11); b, developing gonophore, two-cell stage, SW England (1954.8.3.43); c, mature δ eumedusoid, E Mediterranean, lower shore (redrawn after Kossowska, 1911: fig. 2, as H. billardii); d, undischarged nematocysts, SW England (1954.8.3.43). Scales in a-c = 500 μm; scale in d = 25 μm.

1954.8.3.43). Fully developed 3 and 2 gonophores similar, inverted, medusiform, retained; four branched gastrovascular canals said to be orange in colour. 3 gametes develop in gonads borne on radial canals; mature 2 gonophore contains 3 c. 300 ova. (Description of gonophores based on Hincks, 1868, Kossowska, 1911, and Huvé, 1954.) Developing eggs reported in hydrorhiza in a colony apparently lacking gonophores (Millard & Bouillon, 1973).

MEASUREMENTS. See Table 11.

 $\begin{tabular}{ll} TABLE~II \\ Hydranthea~margarica. & Measurements~in~\mu m \\ \end{tabular}$

	S WALES (1973.3.3.1)	W SCOTLAND (White, 1956; = 1955.11.15.11)	S France (Huvé, 1954)
STOLON			
Diameter	60	60-80	90
Hydranth			
Height (base to hypostome)	200-400*	400-1000	700
Tentacle length		100-170	180
Нурготнеса			
Height (diaphragm to rim)	_		35
Breadth at base	100	80-90	80
Breadth at rim	100	80-90	100
Hydrothecal pedicel	100		150
Nematocysts			
Length		40	30

^{*} Contracted during fixation.

REPRODUCTIVE SEASON. Fertile specimens recorded August (Roscoff, NW France, Teissier, 1965) and October (Plymouth, SW England, White, 1956).

DISTRIBUTION. Recorded from Devon and Dorset, Liverpool Bay, Norfolk and Argyll (White, 1956), mainland Shetland (D. N. Huxtable, pers. comm.), Anglesey (Herdman, 1891), S Wales (present material) and Roscoff, NW France (Teissier, 1965). Elsewhere recorded from the Mediterranean Sea (Kossowska, 1911; Huvé, 1954) and the Seychelles (Millard & Bouillon, 1973).

Habitat. Most frequently recorded epizoic on *Flustra* spp. and other Bryozoa, but also found on hydroids (*Tubularia* sp. and *Halecium* spp.), mollusc shells and bare rock [Hincks, 1868; Kossowska, 1911; Huvé, 1954; White, 1956; Teissier, 1965; present material (1954.8.3.44.)]; also on *Laminaria* holdfasts (D. N. Huxtable, pers. comm.).

Genus OPHIODISSA Stechow, 1919

Ophiodes Hincks, 1866: 421 [non Ophiodes Wagler, 1830 = Reptilia; nec Ophiodes Guénée, 1841 = Lepidoptera; nec Ophiodes Hartig, 1847 = Hymenoptera; nec Ophiodes Murray, 1877 = Arachnida (Marschall, 1873: 266; Stechow, 1919: 41; Neave, 1940: 434)]. Ophiodissa Stechow, 1919: 41 (part) (nom. nov. pro Ophiodes Hincks). Hydrodendron: Millard, 1957: 186 (part).

Type species. Ophiodes mirabilis Hincks, 1866, by monotypy.

DIAGNOSIS. Haleciidae with long capitate nematophore and short nematotheca; hydranth large; hydrotheca wider than deep, rim even; desmocytes conspicuous; gonotheca barrel-shaped, variably rugose, aperture broad, $\delta = \varphi$; no medusa generation; large nematocysts present.

REMARKS. This generic diagnosis agrees with the restriction of Vervoort (1959, 1972) in excluding species lacking a nematotheca. Following Vervoort, the one species concerned is retained in the genus *Hydrodendron* Hincks, 1874a; but as noted by Watson (1969) a review of *Ophiodissa* and related genera is needed and present generic limits are somewhat arbitrary.

Ophiodissa mirabilis (Hincks, 1866)

(Fig. 14)

Ophiodes mirabilis Hincks, 1866: 422-423, pl. 14, figs I-5; Hincks, 1868: 231-233, pl. 45, fig. 2; Teissier, 1965: 20.

Ophiodes caciniformis Ritchie, 1907: 500-501, pl. 23, figs 11-12, pl. 24, fig. 1, pl. 25, fig. 5; Babič, 1913: 473, fig. 7; (syn. nov.).

Ophiodissa mirabilis: Stechow, 1919: 42; Vervoort, 1959: 220.

Ophidissa caciniformis: Stechow, 1919: 42; Vervoort, 1959: 218-221.

Hydrodendron caciniformis: Millard, 1957: 186–187, fig. 3; Ralph, 1958: 342–344, figs 13b-c, 14a; Millard, 1966b: 490–491, fig. 1.

Type material and locality. Holotype: 'on weed', 10–15 m, autumn, 1866, Swanage Bay, Dorset, England; location of material unknown. Neotype: Lower ledges of Capstone, Ilfracombe, Devon, England, lower shore, 1867, infertile colony on four fragments of holdfast of *Laminaria* sp., 1899.5.1.169. The neotype material is labelled 'Ophiodes mirabilis, Ilfracombe, 1867' in Hincks' hand, and is almost certainly the material he cited later (Hincks, 1868: 233).

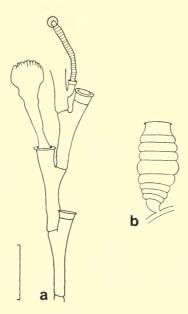


Fig. 14. Ophiodissa mirabilis. a, part of colony with hydranth and nematophore, Cape Verde Islands, 20 m (paralectotype of O. caciniformis, 1964.8.7.92); b, gonotheca, probably SW England (redrawn after Hincks, 1868: pl. 45, fig. 2d). Scale (a) = 500 μ m; (b) unknown.

Other Material examined. Aran Isles, Galway Bay, Eire, 8 Mar. 1899, colonies on bryozoan, in spirit, coll. E. T. Browne, 1954.8.3.40–41.¹⁴ Freshwater West, near Castlemartin, Pembrokeshire, Wales, lower shore, 15 Sep. 1974, young colony on *Dynamena pumila* (Linnaeus, 1758), microslide, coll. P. F. S. Cornelius, 1974.12.17.1. Porto Praya, Santiago, Cape Verde Islands, 20 m, 12 Aug. 1904, two fragments on microslide, coll. J. Ritchie, 1964.8.7.92, paralectotype of *O. caciniformis* (mentioned, Rees & Thursfield, 1965). False Bay, Republic of South Africa, infertile colony on alga, in spirit, coll. N. A. H. Millard, 1957.4.26.23 (mentioned, Millard, 1957, as *O. caciniformis*). Dalebrook, False Bay, Republic of South Africa, LWST, 16 Jan. 1961, infertile colony on brown alga, in spirit, coll. N. A. H. Millard, 1961.6.26.4.

Description. Established colonies irregularly pinnate, loosely polysiphonic basally, up to c. 50 mm but usually less than 20 mm; younger colonies stoloniferous. Hydrorhiza irregularly branched, perisarc thick, with internally-projecting spines; hydrocauli arising erratically. Internodes smooth to slightly wrinkled, hydrophore distal, sloping outwards at c. 45°. Greatest width of hydrotheca c. r_2^1 times depth; rim even, reflexed; desmocytes conspicuous; annular thickening between desmocytes and diaphragm. New hydrothecae arise from side of hydrophore (Millard,

¹⁴ The material bears the locality 'Aran'. Browne's ms diaries in the British Museum (Natural History) show that on the date given his collectors were in the Aran Isles, Galway Bay, and not the Isle of Aran in Donegal.

TABLE 12

Ophiodissa mirabilis. Measurements in µm

SW Indian Ocean Millard, 1966a			I	1	1	1			l	1	1		1	1		l		I	I		1	1		1350	580
SOUTH ATLANTIC SW INDIAN (c. 10°49' N, 16°39' W, OCEAN 42 m; Vervoort, 1959) (Millard, 1966a			1	l	I	1			70-110	1	180-230		1	1				130	06		350-575	1			1
NEW ZEALAND (Ralph, 1958)			1	1	1	I			90-120	6. 250	1		I	I		l		125-187	62		430-750	ı		I	I
South Africa New Zealand (Millard, 1957) (Ralph, 1958)			ı	ı	I	1			85-120	210-240	1		1	ı		1		150~200	10-12		330-540	1		1	I
CAPE VERDE ISLANDS (paralectotype of Ophiodes caciniformis)			(contracted)	(contracted)	(contracted)	(contracted)			40-50	150-170	90-120		500 (1 only)	30 (I only)		60 (I only)		90-120	08-09		450-500	80-100		I	ı
SW England (Neotype)			550-700	120-170	6. 200	30			70-80	180-200	120-130		300-800	40-50		80		120-130	80		350-500	65 - 100			1
	Hydranth	Height (diaphragm	to hypostome)	Greatest width	Tentacle length	Tentacle width	HYDROTHECA	Height (diaphragm	to rim)	Width at rim	Width at base	NEMATOPHORE	Length	Width	Diameter of	terminal knob	NEMATOTHECA	Length	Width at rim	INTERNODE	Length	Minimum diameter	Gonotheca $(3 = 9)$	Height (max.)	Diameter (max.)

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1957; Ralph, 1958). Hydranth large, tapering basally, 18–24 tentacles, held alternately raised and lowered. Nematothecae borne irregularly on internodes, hydrophores and stolon; curved cone-shaped, narrowest basally, sometimes with constriction below rim, both varieties occurring on single colonies; nematophore long, axial cells large, terminal knob with numerous nematocysts including large microbasic mastigophores. Gonothecae apparently recorded only twice. Described as 'ovate, ringed transversely with wide tubular aperture, subpedicellate, borne on stolon', probably ♂ (Hincks, 1866, 1868); similar, but aperture wider, less rugose, ♂ slightly smaller than ♀, no medusa (Millard, 1966b).

MEASUREMENTS. See Table 12.

DISTRIBUTION. Recorded infrequently. From the British Isles, known from Ilfracombe, Devon; Swanage, Dorset (Hincks, 1868; Garstang, 1900); Pembrokeshire (Crothers, 1966; present material) and Aran Isles, Galway Bay (present material). A record from Aberdeen, Scotland (Forbes, 1872), was regarded as dubious by its author. Apparently the only other European record is from Roscoff, NW France (Teissier, 1965). Other records, as O. caciniformis, include the Cape Verde Islands (Ritchie, 1907), South Africa (Millard, 1957), SW Indian Ocean (Millard, 1966b), New Zealand (Ralph, 1958), mid South Atlantic (Vervoort, 1959) and the West Indies (Vervoort, 1968).

Habitat. Most frequently recorded on algae, particularly laminarian holdfasts, but also on other thecate hydroids. Recorded from *Laminaria* zone of intertidal (Hincks, 1868; present material) down to 65 m (Vervoort, 1959).

Remarks. Ophiodissa caciniformis (Ritchie, 1907) is here reduced to a synonym of the present species. O. caciniformis was proposed to include colonies larger than those previously referred to O. mirabilis by Hincks (1868). O. mirabilis has not previously been redescribed; and the larger specimens described by various authors this century have been referred to O. caciniformis. Characters ascribed to O. caciniformis since the original description include an annular thickening of the hydrothecal perisarc below the ring of desmocytes, a goblet-shaped nematotheca and internal projections of the hydrorhizal perisarc (Millard, 1957, 1967; Ralph, 1958; Vervoort, 1959), all of which characters are present in the neotype material of O. mirabilis. Further, the paralectotype specimen of O. caciniformis has all the characters of the older species, and the dimensions of the type specimens of the two taxa are similar. It seems that O. mirabilis was founded on small colonies, and that larger colonies found later were wrongly given specific status.

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